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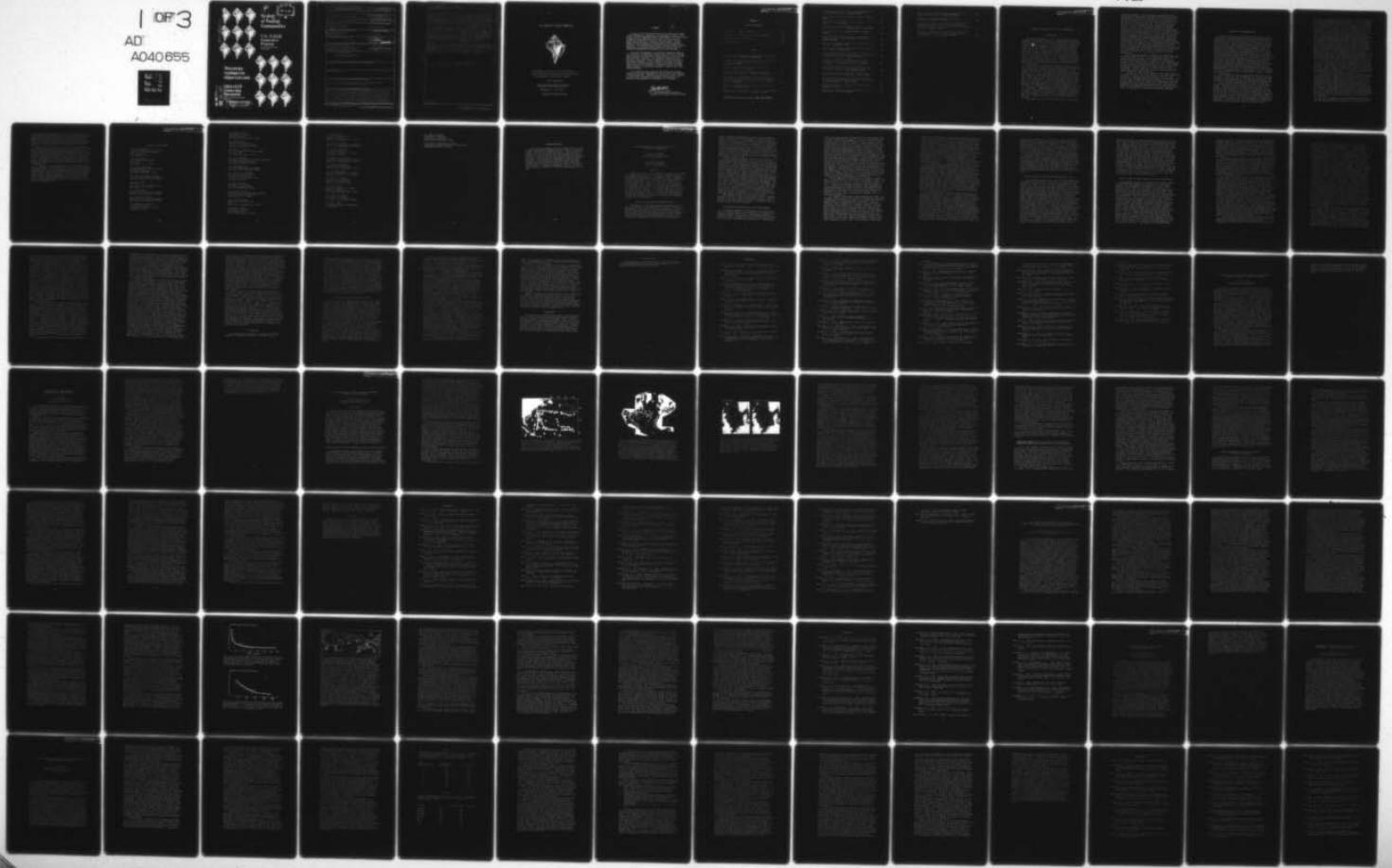
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ECOLOGY OF FOULING COMMUNITIES U.S.--U.S.S.R. COOPERATIVE PROGR--ETC(U)
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Ecology
of Fouling
Communities

U.S.-U.S.S.R.
Cooperative
Program

Beaufort, North Carolina,
U.S.A. 1975

Экология
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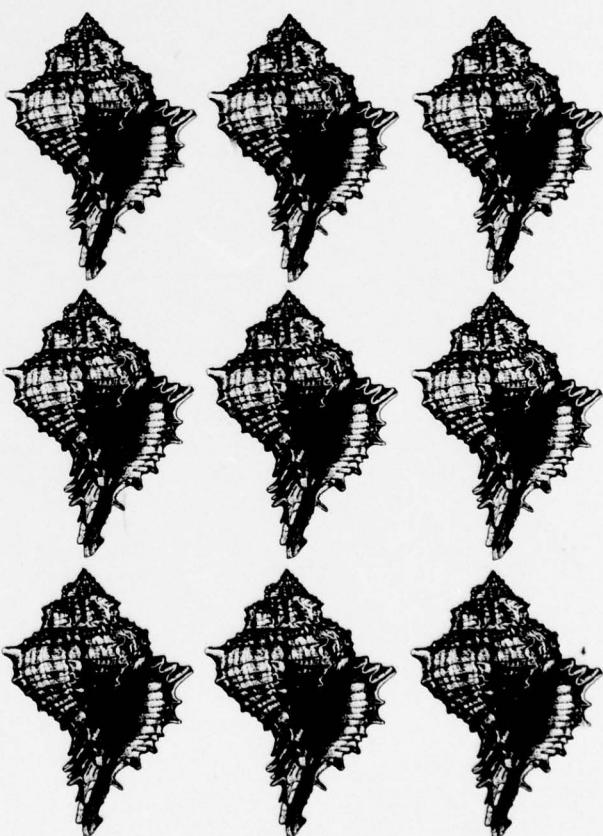
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SECURITY CLASSIFICATION OF THIS PAGE (When Data Entered)

REPORT DOCUMENTATION PAGE		READ INSTRUCTIONS BEFORE COMPLETING FORM
1. REPORT NUMBER	2. GOVT ACCESSION NO.	3. RECIPIENT'S CATALOG NUMBER
4. TITLE (and Subtitle) The Ecology of Fouling Communities Proceedings of the U.S.-U.S.S.R. Workshop within the Program 'Biological Productivity and Biochemistry of the World's Oceans', Held 16-23 November 1975		5. TYPE OF REPORT & PERIOD COVERED Final Report, of Workshop held 16-23 November 1975
7. AUTHOR(s) Editor, John D. Costlow 10	6. PERFORMING ORG. REPORT NUMBER November 1975	
9. PERFORMING ORGANIZATION NAME AND ADDRESS Office of Naval Research Code 484/NORDA Code 440 Arlington, VA 22217		10. PROGRAM ELEMENT, PROJECT, TASK AREA & WORK UNIT NUMBERS NR 104-351
11. CONTROLLING OFFICE NAME AND ADDRESS 13/222 P.		12. REPORT DATE April 1977
14. MONITORING AGENCY NAME & ADDRESS (if different from Controlling Office) Ecology of Fouling Communities U.S.-U.S.S.R. Cooperative Program Beaufort, North Carolina, U.S.A. 1975.		13. NUMBER OF PAGES 232-English, 220-Russian
16. DISTRIBUTION STATEMENT (of this Report) APPROVED FOR PUBLIC RELEASE; DISTRIBUTION UNLIMITED A039 888		15. SECURITY CLASS. (of this report) UNCLASSIFIED
17. DISTRIBUTION STATEMENT (of the abstract entered in Block 20, if different from Report)		
18. SUPPLEMENTARY NOTES		
19. KEY WORDS (Continue on reverse side if necessary and identify by block number) Ecology; Fouling Communities; Biofouling; Boring Organisms; Benthic Communities; Community Dynamics; Invertebrates		
20. ABSTRACT (Continue on reverse side if necessary and identify by block number) Under the US/USSR Agreement in Oceanography, specifically the section on "Biological Productivity and Biochemistry of the World's Oceans," provision has been made for a program to consider the ecology of fouling and boring communities. The basic objectives of the first workshop held at Beaufort, North Carolina, November 16-23 1975, were to review current research in both the United States and the Soviet Union, consider which aspects of the research might warrant further expansion and elaboration, and to plan which phases of the research might be developed into a cooperative program involving (Cont'd)		

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Soviet and U.S. scientists.

Through review papers, abstracts describing specific results of individual research projects, and discussions between twenty five scientists from institutions with the United States and five scientists from institutions within the Soviet Union, current research involving the adult and larval ecology of those species comprising the fouling communities of the world's oceans, were considered. Special emphasis was placed on the interrelationships between the adult and larval stages and how fouling communities are maintained, including the following subtopics: how morphological and physiological characteristics relate to reproductive success of populations and how larval characteristics and behavior, ^{the environment may modify} may be modified by the environment; how the direction and velocity of currents, coupled with behavior, ^{Larval} of the larvae, may affect dispersal between geographically separated populations; taxonomic differences between geographically separated populations of adults; how the genetic basis for differences between and within geographically separated populations, ^{Laboratory experiments may determine} may be determined through laboratory experimentation; the role of larval dispersal in determining the genetic characteristics of populations; and an analysis of niche structure, diversity, and species packing of relevant communities.

In addition to the Introduction and Summary and Recommendations produced by the Workshop, twenty six papers were presented, nine of which are printed in their entirety in this report, while the remainder are represented by abstracts. The official report of the Workshop is a casebound book in which all of the papers are translated in both English and Russian. A preliminary softbound version was produced that contains only the English translation.

This report contains all the English text section included in AD-039 888. The workshop focused on current research on

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THE ECOLOGY OF FOULING COMMUNITIES



Proceedings of the U.S. - U.S.S.R. Workshop
within the Program "Biological Productivity and
Biochemistry of the World's Oceans"

John D. Costlow, Editor

Duke University Marine Laboratory
Beaufort, North Carolina USA

November 16 - 23, 1975

Sponsored by U.S. Office of Naval Research

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FOREWORD

In June of 1973, the United States and the Soviet Union signed a formal agreement for cooperation in oceanographic research. This accord, entitled "Agreement between the Government of the United States of America and the Government of the Union of Soviet Socialist Republics on Cooperation in Studies of the World Ocean" includes working groups on air/sea interaction; ocean dynamics; geology, geophysics, and geochemistry; instrumentation; and biological productivity. The following document on the "Ecology of Marine Fouling Communities" was prepared by the US/USSR Joint Working Group on Biological Productivity and Biochemistry of the World Ocean.

The aim of the Agreement is to encourage cooperative research and an exchange of information between marine scientists of the two countries, not to the exclusion of other nations, but for the betterment of mankind in general. The cooperative program which has resulted in this first volume, is developing in the true spirit of the original agreement: a free exchange of information by marine scientists of the two countries, *in this case* through a workshop held in the US to be followed by a workshop next year in the USSR, leading eventually to the direct exchange of scientists for joint research projects.

It is hoped that this volume will be but the first of many, representing joint and cooperative efforts by marine life scientists of our two countries. Cooperation in such areas of mutual interest can only serve to enhance our knowledge of the oceans and its numerous living communities to the benefit of all mankind.

Robert M. White
Robert M. White, Chairman
U. S. Side US/USSR Joint Committee on
Cooperation in Studies of the World Ocean

Part I

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WORKSHOP ON ECOLOGY OF FOULING COMMUNITIES

Introduction

Within the framework of the cooperative U.S.-Soviet program, "Biological Productivity and Biochemistry of the World's Oceans," provision has been made for a sub-program to consider the ecology of fouling and boring communities. Within this sub-program we have developed several workshops on fouling communities, with a special interest in their origin and stability, their physiological ecology, and their use as an experimental model in lieu of less accessible benthic communities. The basic objectives of the first workshop at Beaufort, North Carolina, November 16-22, 1975, were to review current research in both the United States and the Soviet Union, consider which aspects of the research might warrant further expansion and elaboration, and to plan which phases of the research might be developed into a cooperative program involving Soviet and U.S. scientists.

The community of organisms commonly associated with the "fouling" of man-made structures has been demonstrated to be an excellent system for basic ecological studies, including manipulations and quantitative analysis of the effects of a variety of parameters on community composition and stability. Fouling communities have historically been the focus of a considerable amount of attention with the result that many of the species within this community are well known biologically. Natural communities can be developed on plates which are easily examined and many of the dominant organisms are sessile so that communities can be developed and experiments can be conducted under natural conditions to examine various aspects of community function.

Heretofore, considerations of fouling communities, or for that matter consideration of marine benthic communities in general, have all too frequently restricted themselves to those aspects which involve only the adult populations. The larval phases, as well as the interrelationships between the larvae and adults, have not normally been considered.

The purpose of the first workshop was to consider how

larval development, larval dispersal, and physiological and behavioral aspects of the adult populations can affect the structure and species composition of the community through the control of fluctuations in the population and by the determination of the geographic range and genetic diversity of individual species. To accomplish this it was felt that we should consider a number of dependent aspects: First, how morphological and physiological characteristics of the larvae are related to reproductive success of populations and how the larval characteristics and behavior are modified by the marine environment; Second, how the direction and velocity of ocean currents, together with the behavior of the larvae, affect larval dispersal between geographically separated populations; Third, the taxonomic differences between geographically separated populations of adults (i.e., differences in morphological, physiological, biochemical, and immunological characteristics); Fourth, the genetic basis for differences between and within geographically separated populations of single species through laboratory experimentation; Fifth, the role of larval dispersal in determining the genetic characteristics of populations; and finally, an analysis of niche structure, diversity, and species packing of relevant communities.

It would be hoped that through the review papers, the individual research reports, and the many discussions which occurred during the week of the symposium, some of the interrelationships which exist between the planktonic larvae and the benthic adult communities were examined and further, that some specific thoughts on areas which should be given greater attention have been outlined. Areas where cooperative research would be feasible have also been considered, ideally those areas which would involve U.S. scientists, Soviet scientists, and interested specialists from a number of other countries.

I am hopeful that in the months to come some number of the participants at the first workshop will communicate with each other, outlining in greater detail just how such cooperative programs might be developed. We would then hope to meet again in the Soviet Union, perhaps in the fall or early winter of 1976, to permit those individuals who have developed specific ideas to discuss further the details of cooperative research programs and begin to make definite plans for the exchange of scientists between laboratories in order to implement the projected cooperative programs.

SUMMARY AND RECOMMENDATIONS

Through review papers, abstracts describing specific results of individual research projects, and discussions between twenty five scientists from institutions within the United States and five scientists from institutions within the Soviet Union, current research involving the adult and larval ecology of those species comprising the fouling communities of the world's oceans were considered. Special emphasis was placed on the interrelationships between the adult and larval stages and how fouling communities are maintained, including the following subtopics: How morphological and physiological characteristics relate to reproductive success of populations and how larval characteristics and behavior may be modified by the environment; How the direction and velocity of currents, coupled with behavior of the larvae, may affect dispersal between geographically separated populations; Taxonomic differences between geographically separated populations of adults; How the genetic basis for differences between and within geographically separated populations may be determined through laboratory experimentation; The role of larval dispersal in determining the genetic characteristics of populations; and An analysis of niche structure, diversity, and species packing of relevant communities.

From discussions within individual groups and a final discussion to consider the recommendations of the subgroups, a number of specific areas of research were emphasized with additional recommendations on ways through which coordinated and cooperative research might be initiated and implemented.

A more complete understanding of larval biology was considered essential for an understanding of fouling communities. Emphasis should be placed on studies directed toward an appreciation of the relationship between larval stages and the estuarine and marine environments, including the tolerances and behavior of larvae under laboratory conditions as well as within the natural environment, comparing where possible larvae from populations representing different geographical areas. The basic problems of mechanisms of dispersal, the adaptive role and consequences of widespread dispersal in time and space, and the behavioral adaptations which have been developed by larvae relative to their

planktonic existence should be considered. The mechanisms of larval settlement, including behavior, sensory perception and settlement responses, should receive further consideration and studies on the effects of intraspecific and interspecific interactions at the time of larval settling should be considered as they apply to the effective densities and functional type of adults. Efforts should be made to plan research which concentrates on genetic differentiation of cosmopolitan fouling organisms, with the genera *Mytilus* and *Teredo* serving as examples, and consideration should be given to whether geographical differentiation and magnitude of genetic polymorphism are the same in world wide species as in those species which demonstrate a more restricted distribution. Such studies would contribute a unique series of data on the genetic composition of world wide species and genera, relating directly to the fundamental questions of gene flow, natural selection, migration, and speciation. Within this same general area, studies should be developed which contribute to microgeographic variation (tidal zones, estuaries, etc.) and the relationship of physiology to genetic variability. Life histories and development of deep sea fouling and benthic organisms were also considered to be of extreme importance. The fundamental understanding of larval taxonomy, physiology and endocrinology, were considered as essential to many of the more specialized studies.

It was also felt that further consideration should be given to the structure of fouling communities, both in time and space, including their species composition and biomass. The way in which communities develop in different geographical areas and the types of substratum which they occupy were also considered of importance with further studies to determine the patterns of stability in the different communities and how energy flow and productivity may vary.

Three general phases were considered in the development of collaborative and cooperative research programs. Phase I, which is currently underway, would concentrate on the exchange and further communication of existing information relative to previous and current research on fouling communities. This would include familiarizing participating scientists with existing literature, preparation of review articles with cross publication between the two countries, the planning of workshops and conferences on larval ecology as it relates to the major areas of concern, the exchange of lists of experts indicating areas of interest and species with which they work, and the preparation and dissemination of descriptive and illustrative material on species of mutual interest.

Phase II is viewed as one of exchange of collected material with emphasis on the identification of larvae from both the plankton and from culture in the laboratory plus

the exchange of scientists for relatively short periods of time to permit familiarization with on-going programs, fauna within different areas of the U.S. and the U.S.S.R., and planning for short-term collaborative research projects. Phase II was further viewed as an opportunity for developing cooperative research through the use of on-going research programs of mutual interest to scientists from both countries.

Phase III, developing largely from the short-term collaborative efforts described in Phase II, would lead to planning for specific areas of cooperative research in those areas which have been previously described and where the magnitude of the effort would warrant a carefully organized team research involving scientists from both the U.S. and the U.S.S.R. For example, studies of life histories and development of deep sea fouling and benthic organisms could well require facilities and logistical support which would be best arranged through a joint effort involving scientists from both countries.

It was also felt desirable to develop the long-term program of sampling of fouling communities, utilizing available techniques with the establishment of permanent substrates or quadrants which may be sampled non-destructively, and design experiments to analyze experimentally the species interactions of these fouling communities. Included in this particular portion of the recommended research would be studies on the growth, reproduction, longevity, recruitment, energetics, and genetic variation within the species which form the various communities.

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ACKNOWLEDGEMENTS

The financial support for the workshop and U.S. participants was obtained through the U.S. Office of Naval Research, Contract No. N00014-75-C-1081. Participation by Soviet scientists was made possible through the Soviet Academy of Sciences and the All Soviet Institute of Marine Fisheries. Facilities for the workshop were provided by the Duke University Marine Laboratory, Beaufort, North Carolina. Interpreters and translators were obtained through the Duke Translation Service, Duke University, Durham, North Carolina and thanks are due to the staff of the Institute of Zoology, Leningrad, U.S.S.R. for their final editorial review of the Russian translations of the text.

TOWARD UNDERSTANDING COMPLEX LIFE CYCLES
OF BENTHIC INVERTEBRATES

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INTRODUCTION

Benthic invertebrates exhibit varied patterns of larval development which can include benthic or pelagic larval development and feeding or non-feeding larvae. Energetic efficiency in reproduction, dispersal, and age structure of benthic populations is affected by these complex life cycles; therefore, a theory of structure of fouling communities will not be complete until there is an adequate understanding of the adaptive causes and consequences of these complex life cycles. This review describes some recent work on two aspects of the larval phase which can be expressed as two questions. First, how are costs and advantages of different types of larval development related to the environment or to characteristics of the adults? Second, how is substratum selection related to subsequent survival and reproduction?

COSTS AND ADVANTAGES OF PELAGIC LARVAE

The mortality rates and dispersal associated with pelagic development are different from those with benthic development. The costs of dispersal by means of a pelagic larval stage are transport into areas without suitable habitat for the adults and perhaps also a higher mortality from predation during the pelagic period. It is usually assumed that embryos or larvae which are brooded or sequestered in egg capsules on the bottom do not suffer as

great a mortality as embryos or larvae in the plankton. There are many possible advantages of some means of dispersal in the life of an otherwise sessile or sedentary organism. Offspring which travel some distance from their parents may avoid crowding or concentrations of predators or parasites which occur after a population has been increasing for a period in one area. Local disturbances or other environmental changes may create favorable new areas at some distance from the parental population which can be quickly colonized by dispersing larvae. Spread of offspring relative to each other also occurs during a pelagic phase and can serve to spread the risks encountered during the benthic phase of life.

Pelagic larvae can either feed or rely entirely on reserves provided by the parent. Larval feeding permits growth between liberation from the parent (or egg capsule) and settling. This advantage is usually manifested in the production of smaller and, therefore, more numerous eggs, but sometimes results in larger size at settling. Larval feeding is usually also associated with longer periods of larval development due to limited food supplies, the development of more elaborate larval structures, or both. It is usually assumed that a longer pelagic period results in higher mortality from predation or from transport away from favorable areas. The longer period of larval development also permits greater dispersal, and this is often regarded as a primary advantage of planktotrophic development. In this view, the smaller more numerous eggs and feeding larvae permit greater dispersal at less cost. Currents and eddies in the sea permit dispersal on a rather large scale in a few days (Okubo, 1971), and pelagic periods of this duration are readily attained with non-feeding larvae. There are possible advantages to the added dispersal permitted by larval feeding, but it is not yet clear whether these advantages are commonly realized in nature.

This summary differs only slightly from the views expressed by Thorson (1950) or Mileikovsky (1971). Studies related to the costs and advantages of feeding or non-feeding larvae and benthic or pelagic development are discussed in the following sections.

THE PELAGIC ENVIRONMENT AND LARVAL DEVELOPMENT

An indirect approach to discovering costs and advantages of different modes of development is to examine correlations between type of larval development (benthic, pelagic; feeding, non-feeding) and environmental conditions (latitude, depth, temperature, seasonal food supply, offshore currents, estuarine conditions, etc.). Mileikovsky

(1971) has reviewed work on these trends. The explanations for some trends seem straightforward. The trend toward non-feeding larvae at great depths is probably related to low concentrations of food for larvae. Other trends are less easily explained, such as the trend toward brooded and non-feeding larvae at very high latitudes. Thorson (1946) suggested that the combination of low temperatures and short season of abundant phytoplankton made it difficult to complete larval development while food was abundant. Low food supply results in prolonged development in feeding larvae and, thus, increased risks of mortality from predation or loss from favorable areas. Difficulties of this explanation have been discussed by several authors. Thorson himself pointed out that some widespread and abundant species at high latitudes have feeding pelagic larvae. Pearse (1965, 1969) argues that some of these feeding larvae may be demersal and require periods on the order of one year to complete larval development. Underwood (1974) argues that development rates are adapted to environmental temperatures and that rate of development of feeding larvae is limited more by food supply than temperature. This argument is only partly correct, and because it concerns costs of a pelagic feeding larval stage under less extreme conditions, it is worth noting studies concerning rates of development and temperature.

Partial temperature compensation in rates of development is described for times between cleavages in summer and winter eggs of *Paracentrotus lividus* (Horstadius, 1975), for time to hatching in several species of copepods (McLaren, et al., 1969), and for other organisms, but development is still slower for the animals living at lower temperatures. Slower development at lower but normal environmental temperatures has been found in other inter- and intraspecific comparisons of embryos. (See Patel and Crisp, 1960, on barnacles; Pearse, 1969, on asteroids; and Wear, 1974, on a decapod crustacean.)

The studies cited above concern non-feeding stages. In culture, feeding larval stages from colder waters also tend to develop more slowly at or near their normal environmental temperatures. The counterexample frequently cited is Thorson's (1946) comparison of pelagic larval periods in echinoderms from tropical and temperate waters. Thorson noted that many of the larval periods with feeding larvae were similar, but these estimates were from cultures in which temperature and food varied greatly. If the minimum pelagic periods listed by Thorson are compared, the echinoderms from warmer waters clearly developed faster. The same result is obtained when other studies of echinoderms with feeding larvae are compared (Caldwell, personal communication; Greer, 1962; Johnson and Johnson, 1950; Turner, 1965; Yamaguchi, 1973). Most results from the laboratory

have limited relevance to the problem, however, because the nature and concentration of food are unlike natural conditions. It is curious that there have been few attempts at coastal laboratories to estimate the degree to which naturally occurring food limits rate of development of planktotrophic larvae. Vance (unpublished) used unfiltered sea water changed daily to rear echinoplutei and compared rates of development in these cultures to rates in similar cultures in which phytoplankton concentrations were reduced by addition of filtered sea water. He found that a decrease in phytoplankton concentration prolonged development. If development rates were increased by addition of cultured phytoplankton or concentrated phytoplankton, then food limitation under natural conditions would be clearly demonstrated. Such experiments could be carried out for many types of larvae in many waters without great difficulty.

If rates of development and mortality could be readily determined from plankton samples, the results would be far more relevant to determining the costs and advantages of different types of larval development. Such estimates are possible when all stages considered can be caught with equal efficiency and when larvae are produced synchronously in discrete pulses. When larvae are produced continuously at a constant rate, the mortality between stages can be estimated but not rate of growth. Mileikovsky (1971) discusses several studies in which mortality was estimated from plankton samples, but there is not sufficient data for comparisons among larval types or among locations. Comparative data obtained in this manner for different taxa and different waters would be of great interest, but few attempts have been made. Only data from the field can demonstrate effects of larval size or defense mechanisms on mortality rates in natural populations.

The discussion above indicates some difficulties in using observed geographic trends in type of development to determine advantages and costs of different types of larval development. Another source of difficulties in interpreting correlations with environmental gradients is that so many factors vary together. Temperature and concentrations of food often vary simultaneously and comparisons among locations in which these two factors are separated require more advanced planning of sampling and observation than has been possible to date. Different types of larval development can be associated with different sizes at metamorphosis so that a shift to another mode of larval development might be caused by selection for larger size in individuals beginning benthic life. In asteroids with non-feeding larvae (either brooded or pelagic) the juveniles formed at metamorphosis tend to be much larger than the juveniles formed by planktotrophic development (Birkeland, *et al.*, 1971). In

ophiuroids with brooding, the juveniles released from parents tend to be larger than juveniles formed at metamorphosis of either feeding or non-feeding larvae developing independently of the parents (Hendler, 1975). The value of larval dispersal may also vary over environmental gradients because of trends in the dynamics of benthic populations. There is not sufficient information to rule out the possibility that advantages of a dispersal phase, as well as costs of a dispersal phase, may determine observed trends.

Finally, the forms of feeding larvae are conservative, and different larval forms may exhibit different inherent limitations in their feeding mechanisms (Strathmann, 1975). The larvae of reptant decapods prey on animals rather than on phytoplankton and may not experience the same limitations on food supply over the same environmental gradients. This could contribute to the higher incidence of planktotrophy among decapods as compared to taxa with ciliated larval forms, but hypotheses of this sort can be tested only by extensive comparative observations utilizing numerous higher taxa.

SIZE OF EGGS IN SPECIES WITH PLANKTOTROPHIC LARVAE

Larval feeding permits small eggs and, therefore, numerous eggs, but the causes of variation in size of eggs among species with planktotrophic larvae has not received much attention. Vance's (1973) model of "strategies" of reproduction with lecithotrophic or planktotrophic larvae emphasized energetic efficiency and the advantages of either extreme planktotrophy with very small eggs or complete lecithotrophy with no feeding, but the cost of reducing egg size when there is planktotrophic development has not been examined adequately for benthic invertebrates. Blaxter and Hempel (1963) found that herring eggs with greater dry weight develop to hatching in the same time but give rise to larvae which are longer and heavier, have a larger yolk sac remaining at hatching, and survive longer while starving. To my knowledge, survival while starving has not been examined in relation to egg size in benthic invertebrates, though information on rate of development and larval size is available. Indirect estimates on volume filtered per milliliter of oxygen consumed for two echinoids with different sized eggs indicate that small eggs need not impose a decreased efficiency of feeding (Strathmann, 1975). Smaller larvae generally are restricted to smaller food and this may be one of the greatest costs of reduced size of eggs. McLaren, *et al.*, (1969) find that larger eggs develop more slowly through hatching in copepods, and Wear (1974) indicates that this may be the case among closely related

decapod crustacea; but egg size does not discernibly influence time to hatching in many invertebrates with feeding larvae. Vance's (1973) model assumes that decreased egg size with planktotrophy necessitates a longer larval life. This might indeed be expected if the size of the juvenile formed at metamorphosis were always the same, but this size can vary greatly. In some taxa smaller eggs produce smaller hatched larvae and smaller larvae at settling (Barnes and Barnes, 1965, on barnacles) and an effect on the length of pelagic life has not been detected. In such cases both larger food available to the larva and larger size at the beginning of benthic life could provide an advantage to animals with larger eggs. In other taxa, stage and size at settling and metamorphosis can vary greatly and may be largely independent of egg size. Larger eggs can be associated with higher latitudes and colder water within a species or a genus with a feeding larval stage (Barnes and Barnes, 1965, on *Balanus balanoides*; Efford, 1969, on *Emerita* spp.; Hagström and Lönnning, 1967, on *Strongylocentrotus* spp.). The adaptive significance of these gradients in egg size could involve any of the factors mentioned above.

PELAGIC LARVAE AND THE DYNAMICS OF BENTHIC POPULATIONS

The absence, presence, or duration of a pelagic larval phase undoubtedly affects the dynamics of benthic populations, and the dynamics of populations in the benthic phase of life undoubtedly influences the evolution of pelagic larvae; but it is difficult to distinguish causes and effects in these relationships. Thorson (1946) suggested that species with a long pelagic larval phase had more irregular annual recruitment because of varying success in the plankton. Barnes and Powell (1950) suggested that a heavy set of *Balanus balanoides* could result in over-crowding and loss of hummocks, and that a light set could result in firmer attachment and higher survival rates in the benthos. Many other investigators have also interpreted spatial and temporal variation in benthic populations as the result of variations in intensity of set of larvae. Most authors drawing this conclusion, however, were unable to observe mortality of the newly settled juveniles. Connell (1961) followed settling and survival of *B. balanoides* cyprids and concluded that "while the density observed at the end of the settlement season may occasionally be severely limited by the supply of planktonic larvae at Millport it was usually determined by occurrences on the shore, there being a vast oversupply of larvae." Muus (1973) in a study of 11 bivalve species in the Øresund found that "the number of settling bivalve

specimens had very little influence upon the success of the season's spatfall." Sampling and counting settling larvae or newly settled juveniles is tedious, for some species it is impossible, but it is the most reliable means of distinguishing losses in the plankton and losses in the benthos. Investigators who have attempted such sampling have found a great degree of independence between intensity of set and numbers subsequently surviving to reproduce. Though appropriate studies have been few, we can conclude that although set varies enormously, benthic conditions also impose large variations.

The studies mentioned above do not compare animals with feeding and non-feeding larvae or brooded and pelagic development; but if benthic conditions can produce large variations in recruitment, the size and development of juveniles when they begin benthic life or the habitat occupied in the benthic phase may have as great an influence on variation in recruitment as the duration of the pelagic larval stage. Buchanan's (1967) studies on five species of infaunal echinoderms indicated no relationship between the type of larval development and annual variation in the adult population (Strathmann, 1976).

As indicated above, the data from most studies do not separate variations in survival in the plankton, success in settling, and survival in the benthos, yet these distinctions are essential to an understanding of the adaptive significance of larval dispersal. Four other obstacles to such understanding are the difficulty of studying populations over large areas and long periods, the difficulty of determining survival of different genotypes, confusion concerning different sorts of advantages to be gained from dispersal, and the difficulty of determining the actual dispersal of larvae released at various locations. The latter two obstacles are discussed below. A sessile organism obviously requires some means of dispersal at some stage of life. The advantage to be gained from a pelagic period of several weeks, as opposed to several days, is less obvious. Scheltema (1971) has emphasized the distance larvae may travel from their parents and implies that differential extinction of populations or species may favor species with a long pelagic larval phase. Such differential extinction could result from the ability of animals with long-distance larvae to colonize new areas and extend their range or from the long-distance dispersers being "generalists" capable of living in a greater range of habitats and hence able to withstand changing conditions.

A very different sort of advantage from dispersal emphasizes the spread of siblings relative to each other and selection among individuals within a population (Strathmann, 1974). When the favorability of areas varies

independently or inversely so that one year, one place is better and another year, another place is better, then parents spreading their offspring over all such areas gain an advantage over several generations. This advantage arises because averaging variations over space results in a more even success over time. The dispersers can gain a relatively greater multiplication over generations than that obtained by animals with more limited dispersal, even when the dispersers' mean success per generation is less. This hypothesis implies that the advantages of dispersal might be felt over shorter periods. Other factors than longer pelagic period can enhance spread of offspring relative to each other. Variation in length of pelagic life, variation in vertical position, and spread in times of larval release all enhance spread of siblings (Strathmann, 1974) so that interpretations of spawning, development rates, and swimming behavior are somewhat altered under this hypothesis. This hypothesis also implies that altering natural patterns of spatial and temporal variation could change the representation of many species in benthic communities over several generations. It should be noted that these two hypotheses do not exhaust the possible advantages of large scale dispersal and are not mutually exclusive. Testing these hypotheses is difficult but not impossible. Differential extinction of species cannot be observed directly but might someday be inferred from the fossil record. Larvae of bivalves and gastropods can be preserved as fossils, both as part of the shells of well preserved adults (Shuto, 1974) and as larvae before metamorphosis (Jung, 1975; LaBarbera, 1974). In many mollusks, inferences about length of pelagic period can be drawn from the size and form of the larval shells (Ockelman, 1965; Shuto, 1974; Thorson, 1946). The second hypothesis might be tested more directly by monitoring variations in survival and reproduction over large areas for many years in favorable situations with favorable animals. Less direct approaches can strengthen the case for accepting or rejecting these and other hypotheses on the adaptive advantage of dispersal.

In many species the large scale dispersal resulting from a long pelagic period may be of no advantage but rather an accidental result of a pattern of development favored for other reasons. Vance (1973) offers a model of planktotrophy and lecithotrophy in which dispersal is ignored. In this model there are conditions of food supply and mortality rates in the larval phase under which either extreme planktotrophy or extreme lecithotrophy is favored and intermediate "strategies" are at a disadvantage. Though some assumptions of this model are not realistic, its general form and conclusions are of interest. Many holoplanktonic copepods exhibit feeding larval stages similar to those of barnacles,

and it is not necessary to invoke an advantage from dispersal to account for such larval stages in copepods. Some benthic invertebrates with feeding larvae and rather long larval periods have demersal larvae and presumably restricted dispersal. (See Mileikovsky, 1971, for review.)

Larval dispersal is not easily observed. There are observations indicating the distances larvae can move from the parental population, but no one has determined the distance larvae move from their parents or their siblings. All three kinds of dispersal are of interest because each is related to a different set of advantages and costs and different practical consequences. Scheltema (1971) has obtained evidence for the trans-Atlantic transport of larvae of shallow water invertebrates and provided an estimate of the fraction successfully completing the crossing. Scheltema's observations provide a strong contrast to Crisp's (1958) description of the invasion of the British Isles by the barnacle *Elminius modestus*. Crisp found that 30 kilometers of deep water was a moderately effective barrier. Crisp also noted an extension of range of about 20 to 30 km per year in the absence of strong favoring currents. This rate of spread depends on the generation time and frequency of reproduction of the barnacles as well as the dispersal of the larvae, but gives some idea of the rate of spread of an animal's descendants through a population when there is a pelagic stage of several weeks. Most other observations of dispersal are also based on offshore transport of larvae or extension of ranges of adult distribution.

Studies of eddy diffusion indicate expected rates of spread of larvae relative to their siblings, and studies of currents indicate expected transport away from parents, but vertical swimming can make a great difference in dispersal. The importance of vertical position has been particularly emphasized in studies of estuarine invertebrates (Bousfield, 1955; Haskin, 1964; Hughes, 1972; Wood and Hargis, 1971). Both spread of siblings and position of all larvae in the estuary are determined by the movement of larvae into surface outflow, into more saline bottom water, or onto the bottom itself. It should be noted, however, that Banse (1964) found larvae to be bound to water layers in an area of stratified water and suggested that these larvae may have continued life in the water in which they were first released. Variation in swimming within populations has been described by Doyle (1974) and George (1967). George inferred that differences within a brood in the behavior of larvae of a cirratulid polychaete were genetically determined. Doyle was able to employ breeding experiments on *Spirorbis borealis* to demonstrate heritability of differences in larval response to light.

When offspring travel far from their parents they can

be subject to quite different selective pressures from those affecting their parents. This can affect interspecific interactions and, hence, the structure of benthic communities. "Finely tuned" coadaptive mechanisms can arise when members of different species interact over many generations. In some species with a long pelagic larval phase, the offspring settle in communities quite different from the parents'. An extreme example is provided by those invertebrates which settle and survive in waters too cold for their successful reproduction. (See Williamson's, 1967, review of a decapod crustacean in northwest Europe.) These individuals are as good as dead in an evolutionary sense. Members of other species may evolve better means of coping with these animals, but there can be no co-evolution in the non-reproducing populations.

Fecundity and longevity of adults may also be related to the type of development. A mode of larval development which resulted in frequently poor recruitment over large areas would require an adult phase with long life and repeated reproduction. Size of adults may also place constraints on type of larval development. Chia (1970, 1971) maintains that invertebrates with feeding larvae devote more energy to reproduction than invertebrates with lecithotrophic development and that some species can persist only with lecithotrophic development because of limited energy or material which can be devoted to reproduction. Menge (1975) argues that some species are small because they are adapted for coexistence with larger dominant competitors and that small size limits the material which can be devoted to reproduction; these species must increase their efficiency of reproduction by brooding their offspring and forgo larval dispersal. Both authors present supporting data from a limited number of species. There appear to be awkward implications in both these arguments. If brooding or lecithotrophy offers a more reliable and higher return of juveniles, shouldn't all the species in these studies adopt such a mode of reproduction? Menge suggests that pelagic larvae offer a different kind of advantage related to the greater dispersal, but he does not say what kind of advantage or mention the scale of time over which it would be manifested. If the enhanced dispersal offers an advantage over a short period of several years, as could occur with spread of siblings when favorability of habitats varies independently or inversely (Strathmann, 1974), then the advantage is likely to involve survival and reproduction of offspring at least equal to those animals with more limited dispersal. Longer life may be required of such a disperser but not a greater annual reproductive output. We do not see this approximately equal efficiency of return because our studies are limited to a few locations and only a few generations.

If such short term benefits are the principal advantage of larval dispersal, then why cannot the smaller species (or in Chia's argument, the energy limited species) be equally capable of partaking of this advantage, for the recruitment will be as great when a sufficiently large geographic scale or period of time is considered. If the enhanced dispersal offers an advantage only over long periods, as would be the case with differential extinction of populations or species, then species forced into brooding or lecithotrophy are temporarily avoiding an extinction which will occur later unless conditions change. Trends in adult size and brooding would be more satisfactorily explained by demonstrating that brooding becomes more difficult or costly relative to pelagic development with greater adult size. M. Strathmann (personal communication) has suggested that if fecundity is volume dependent and brooding capacity more dependent on area, larger animals can brood a smaller fraction of what they could produce. Both Chia and Menge have presented intriguing data and interpretations, but more extensive observations and discussion of the subject is badly needed.

Another possible influence of benthic conditions on pelagic period and type of development arises from the influence of adult condition on larval viability or rate of development. Bayne (1972), Bayne, et al., (1975), and Helm, et al., (1973) found that nutritive stress in adult bivalves resulted in decreased viability of offspring in the pelagic phase. Bayne, et al., studied *Mytilus edulis*; Helm, et al., *Ostrea edulis*. Helm, et al., found that growth rate in the first 96 hours after liberation of larvae was also affected, with growth rate related to lipid reserves in the larvae. Bayne, et al., did not find a significant relation between growth and lipid reserves in the larvae and did not find such a strong relation between growth rate of feeding larvae and nutritive stress in the adults. It is not yet clear whether effects such as these are important in nature and whether the effects vary with type of larval development. Food supply of adults can vary with crowding or location, and comparative observations of larvae reared from adults from differing locations could clarify this link between conditions in the benthos and success in the plankton.

FLEXIBILITY

The occurrence of brooding or pelagic development, feeding or non-feeding larvae in a species may have

important adaptive consequences for all species of benthic invertebrates, but some taxa may possess more flexibility than others in shifting from one pattern of development to another. Hadfield (1972) has noted two instances of flexibility in shifting from a completely non-pelagic to a pelagic larval development, both among gastropods. Gastropods often retain the velum and velar cilia of pelagic larvae even when veliger larvae are retained in egg capsules and may thereby retain greater flexibility in evolving from non-pelagic to pelagic development. Numbers of nurse eggs can vary greatly, and spionid polychaetes and gastropods employing nurse eggs may possess flexibility in the larval phase, shifting to or away from a pelagic development. In contrast, all but a few echinoderms with brooded or non-feeding pelagic larvae have completely lost the structures needed for larval feeding. In this phylum, once a feeding larval stage is lost it is not regained. This inflexibility could lead to relatively maladapted life histories in some taxa (Strathmann, 1975). In searching for patterns of larval adaptation, one should avoid taxa in which such accidents of history and ancestry are likely.

CUING, SETTLING, AND BENTHIC SUCCESS

Pelagic larvae of sedentary invertebrates must select the spot in which they take up benthic life. Their subsequent survival and reproductive success depends on their ability to predict the favorability of a spot from the limited cues available to them. Crisp (1974) has recently reviewed the sorts of cues used by larvae. Larvae in all major taxa can delay settling in the absence of a suitable substratum. Many larvae become less specific in their choice of substrum as the period of delay increases. This may represent a balance between the risks of continued pelagic life while awaiting a better spot and the risks associated with less favored substrata (Doyle, 1975).

The adequacy of the cues used by larvae can be examined by following their subsequent survival and reproduction. For example, cyprids of *Balanus balanoides* prefer to settle in pits or cracks (Crisp and Barnes, 1954) and survival is better in such locations than on convex surfaces (Connell, 1961). Stebbing (1972) found that bryozoan and serpulid larvae settle preferentially on the younger parts of *Laminaria* fronds and suggested, first, that since the younger parts last longer, the possible length of life of the animals is increased and, second, that their choice could reduce crowding. These examples indicate an ability to make fine distinctions in detecting cues to favorable substrata.

Lack of specificity in larval settlement can also be adaptive. Hurley (1973) found that larvae of *Balanus pacificus* settle readily on a great variety of substrata, in contrast to the greater specificity found in *Balanus balanoides* by Barnes, Crisp, Knight-Jones and others. Hurley also found that *Balanus pacificus* is an opportunistic species with fast growth and early reproduction and its persistence may depend on its temporary colonizing of new substrata not yet colonized by other animals.

Intraspecific variation in preference for substrata is also being examined and reveals complexity in optimal cuing. Knight-Jones, et al., (1971) found different preferences in larvae from different areas. The larvae of *Spirorbis borealis* settled preferentially on *Fucus vesiculosus* or *Fucus serratus* depending on the favorability and abundance of the algal species in each area. The difference in preference is probably genetic. Doyle (1975) has provided a model in which the advantage of varied substratum preferences depends on the risks of delaying metamorphosis, the probability of encountering and surviving on each type of substratum, and the spatial distribution of mixtures of the types of substrata. His preliminary observations on choice of algal substratum by *Spirorbis borealis* are consistent with his model. *Spirorbis* has a short pelagic period. Local differences in preferences for substrata are less likely when dispersal is greater.

Within a population, some genotypes survive better in one habitat, others in another. If each type settled preferentially in the habitat for which it is best suited, the selective deaths increasing the cost of dispersal would be minimized. This might be accomplished by appropriate linkages of genes, but this has not been demonstrated to occur. Struhsaker (1968) examined a polymorphism in *Littorina picta* in which the frequency of rough-shelled individuals and smooth-shelled individuals varied with the type of shore and wave force. Larval rearing showed that the differences in shell type were inherited. At a given location, very young snails exhibited greater variation in shell type than older snails. It thus appears that larvae of both types settled on both types of shore and selective deaths produced the observed distribution. It is likely that in this population selective deaths impose a higher cost on dispersal because the different morphs do not preferentially settle on the substratum best suited for them.

Poor choices by larvae can be either the result of inability to detect relevant cues or the absence of relevant cues. Hayward and Harvey (1974) note that the bryozoan *Alcyonidium* settles preferentially in the grooves on *Fucus serratus*, which appears to be a favorable area, but also settles in necrotic depressions on the flat part of the

blade, which enlarge so that bryozoans settling there are lost. A response that is usually adaptive for the bryozoans is unadaptive in this instance.

Balanus glandula may provide an example of difficulties of cuing on a larger geographic scale. Connell (1970) found that *B. glandula* on rocky shores in the San Juan Islands settle in both the upper and middle intertidal, but survive to reproduction only in the upper intertidal. The same is true on rocky shores of the open coast of Washington. The barnacles' difficulty in cuing for the appropriate intertidal range may arise from the different pattern of success on rocks surrounded by sand or mud or rocky shores on protected bays, as in Puget Sound. In these areas many *B. glandula* survive to reproduce in the middle and lower intertidal. Exchange of larvae between these types of areas may prevent the evolution of more precise cuing to the upper zone of exposed rocky shores. Man-made structures have increased the extent of favorable low intertidal habitat and may even have changed the optimum specificity of cuing in this species.

There is little direct evidence that larval preferences for types of substratum result in selection of the more favored substratum when each type covers a large area. Muus's (1973) study of infaunal bivalves comes closest. The water carrying the larvae passed over both areas sampled, but very young juveniles of several species were abundant in only one area or the other; so unless there were extreme differences in early mortality, many of the larvae rejected one area to settle in the next encountered.

CONCLUSION

This review has considered the adaptive significance of pelagic larvae in terms of relationships between different parts of complex life cycles and between types of larval development and the pelagic environment. There are clearly many hypotheses for the adaptive significance of these life cycles and a shortage of quantitative comparative studies designed to test these hypotheses. The patterns of larval dispersal and variations in the benthos favoring such dispersal are particularly difficult to observe and present the greatest obstacles to understanding these life cycles.

Acknowledgments

The preparation of this review was aided by discussions with investigators at the Friday Harbor Laboratories and by support from N.S.F. Grant DES 74-21498.

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STUDIES ON THE BEHAVIOR AND PHYSIOLOGY OF RESPONSES
TO LIGHT AND GRAVITY BY LARVAL CRUSTACEANS

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Behavioral responses to light and gravity by free-swimming larvae of benthic crustaceans throughout development are currently being investigated. Species which occur throughout the estuaries and coastal areas are studied for comparative purposes, but the primary experimental animal is the crab *Rhithropanopeus harrisii*. Due to their small size and occasional rapid movements, the larvae's behavior is monitored by a microscope-closed circuit television system.

R. harrisii zoeae respond to both directional light (phototaxis), and to polarized light (polarotaxis). Like most crustacean larvae found in coastal areas, the primary spectral sensitivity maximum occurs in the green region. The sign of phototaxis at different light intensities is similar at all zoeal stages and for light-adapted larvae phototaxis consists of a positive response to higher intensity which becomes negative at low intensities. The negative response disappears after dark-adaptation. Based upon these phototactic responses, the predicted diurnal vertical migration pattern for such larvae is a rise during the day and a descent at night. Further studies of behavioral responses upon intensity decreases demonstrate that crab zoeae have a predator avoidance shadow reflex which could function in nature to avoid ctenophores. The avoidance pattern, upon an intensity decrease, consists of a positive geotaxis, involving passive sinking.

Temperature and salinity are two environmental factors which influence the vertical distribution of zoeae and thereby, potentially contribute to horizontal movements in water currents at different depths. For *R. harrisii* larvae, sudden exposure to temperature does not alter phototaxis. Nevertheless, high temperatures which usually occur near the surface do induce a positive geotaxis and thereby can be avoided. Similarly, low salinities which usually occur near the surface also would be avoided, since sudden exposure induces positive geotaxis and negative phototaxis. Sudden

exposure to high salinity water causes no change in phototaxis, but induces an ascent due to a pronounced negative geotaxis. These studies serve as a means for determining which behaviors and environmental factors contribute to vertical movement and horizontal transport of crustacean larvae.

BIVALVE LARVAE, THEIR BEHAVIOR,
DISPERSAL AND IDENTIFICATION

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The distribution, ecology and population dynamics of a species can be understood fully only when its life history is known, making identification of all stages possible. Different but equally important selective pressures on the larvae, metamorphosing young and adults of benthic marine organisms are reflected in their reproductive success and distribution.

Males of most sessile and infaunal marine invertebrates release sperm into the sea, though a few transfer it directly as in the teredinid genus *Bankia* and the barnacles, *Balanus*. A unique adaptation to insure fertilization is seen in *Psiloteredo megatara*, a species found in floating wood. The male extrudes a large diaphanous sperm sac which is taken in by the female's extended 'searching' incurrent siphon. Protection of the young varies but brooding species are always the smallest in the family.

Much has been written on the types of invertebrate larvae (planktotrophic, lecithotrophic, non-pelagic and demersal), their adaptive value and their importance in genetic exchange and in the dispersal of the species. Among molluscs, gastropod larvae have received particular attention probably because they are relatively easy to identify. Bivalves constitute a major component of the larvae of benthic marine organisms taken in plankton tows but they usually are not identified or at best only to family or genus, mainly because they have few identifying characters. Unlike the larval shells of gastropods, which are often visible at the apex of the young adults, the prodiscoconchs of bivalves are soon buried in the umbos of the growing young. Consequently even young spat in museum collections are of little help in identification.

There are two ways of studying and identifying bivalve larvae: (1) collect them from the plankton and rear them individually to an identifiable stage, (2) spawn known

adults and rear larvae in mass cultures to young adults. Either way the various stages should be documented continuously by careful measurements and photographs of both living and preserved larvae. We have used both methods and found that larvae are often more easily identified by their swimming and crawling behavior than by their shells. Observations of the valves using SEM show that closely related species have distinctive sculptural and hinge characters not visible with the light microscope. Larval characters such as the ventral tooth and socket present in the pediveliger stage of *Zirfaea* and *Martesia* may point to unsuspected phylogenetic relationships. Measurements of the valves of 4 large populations of *Martesia striata* larvae from 4 different female parents (all cultures were fertilized by the same male) differed up to 28 μ in mean shell length and showed that the size of the pediveligers varies considerably. Since size is typically used to distinguish species of bivalve larvae it is important that shell size data be based on multiple rearings from different parents.

Observations of living larvae suggest that (1) planktrophic larvae living in rich inshore waters have proportionately smaller velar lobes than those adapted for living in plankton poor oceanic waters, (2) larvae of brooders have shorter apical flagella than oviparous species and (3) when bivalve larvae first begin to swim they are temperature sensitive and select their optimum temperature in the water column. This may function to keep them in areas of maximum food and to hold demersal larvae near the bottom.

Larviparous species or those with egg capsule development have a more restricted range than their planktotrophic cousins unless they have other means of dispersal, e.g. floating wood, ships or pumice. Adults of the latter group of species, including many wood boring and fouling organisms, generally have a wide temperature tolerance and the ability to retain larvae until conditions are optimal for survival. The young of these species emerge in the settling stage and can immediately join their parents on or in the same substrate. Conversely larvae of oviparous fouling species spawned in mid-ocean must spend a month or more in the plankton and are lost at sea for want of a substrate at time of settlement.

Most models of reproductive strategy place emphasis on predation of the larvae in the plankton but we find that the greatest mortality often occurs at the time of settlement. For metamorphosing invertebrates this is a period of great anatomical and physiological change. Though the ability to delay metamorphosis, if the proper substrate is not available, is an important factor in the survival of many larvae, the effect of false 'triggers' such as 'gelbstoff' on *Teredo navalis* pediveligers can be

devastating. Once metamorphosis has begun the loss of larval organs and the development of new ones must follow in a precise sequence. Delay, disruption or blocking of any step whether it be physical or chemical results in malformation or death; e.g. the presence of obtusaquinone in rosewood (*Dalbergia*) does not prevent the settlement of teredinid pediveligers but effectively stops further metamorphosis and penetration of the wood by blocking the enzyme phenoloxidase and so the development of the shell.

THE SIGNIFICANCE OF PELAGIC LARVAL DEVELOPMENT
TO MARINE FOULING ORGANISMS

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INTRODUCTION

Almost all marine fouling organisms have some form of free-living larval stage. The length of the pelagic stage differs widely among various invertebrate species from a few hours, as occurs among serpulid worms, to several weeks, characteristic for barnacles, or even six months to a year for some tropical species (Scheltema, 1971b). The principal biological significance of this pelagic larval development to marine fouling organisms can be conveniently summarized in three points. First, planktonic larvae maintain the distribution of a species and also present the constant possibility of enlarging the geographical range when additional habitat becomes available. Second, by their dispersal larvae implement genetic exchange (or so-called gene flow) between populations thereby influencing the amount of genetically determined geographic variation found within species. Third, larvae serve in habitat selection, that is, they determine through the act of settlement the place where the adult sessile forms will become permanently attached; consequently, larvae may influence the intra- and inter-specific associations within fouling communities.

LARVAL DISPERSAL AND THE GEOGRAPHIC RANGE OF FOULING SPECIES

Compelling evidence that pelagic larvae are a means whereby sedentary invertebrate organisms can be dispersed along coastlines and even across zoogeographic barriers such as ocean basins comes from the knowledge that larval stages occur regularly within all temperate and tropical near-shore waters, over continental shelves, in shallow enclosed seas, and within the major oceanic current systems. Research within the last fifteen years by Mileikovsky (1966),

Robertson (1964), and Scheltema (1964, 1968, 1971a, 1972) has shown that certain teleplanic larvae, that is, "long-distance" larvae from shoal-water sedentary organisms of coastal regions, can be carried over thousands of kilometers in the open sea and, moreover, that species having such widely dispersed larvae are also those with very wide geographical ranges. Examples of teleplanic larvae described in the literature are mostly of species from benthic communities.

There are also, however, larvae of fouling organisms that are extensively dispersed in the open sea, for example, the cyphonautes larvae of encrusting cheilostomous bryozoans can be found throughout the Gulf Stream and Sargasso Sea (Fig. 1). These larvae, although not presently identified, probably belong mostly to *Membranipora tuberculata* Busk, a species habitually found on *Sargassum* weed in the open seas. Other kinds of larvae belonging to fouling organisms and commonly found in the open ocean are the nauplii and cyprids of goose-neck barnacles belonging mostly to the genus *Lepas* and *Choncoderma* (Fig. 2). Adult barnacles of both these genera are also found far out at sea attached to drifting objects. Veliger larvae of the wood-boring Teredinidae or shipworms occur in open waters of the temperate and tropical Atlantic Ocean (Scheltema, 1971c), and representatives of at least two genera can be found.

The dispersal of fouling organisms by means of pelagic larvae may be augmented, or in some instances entirely replaced, by the rafting of adults on floating objects. Indeed, it is only among fouling organisms that rafting is likely to be a significant mode of dispersal. In the three examples of oceanic larval dispersal just given, *viz.* bryozoa, barnacles, and shipworms, there also exists the capability of long-distance rafting. Certain species of fouling organisms with very short pelagic larval life must surely have attained their wide geographic range solely by this means; the shipworm *Lyrodus pedicellatus*, with a one-day larval stage and a circumtropical distribution, is an example of rafting in wood (Turner, 1966). Coelenterate hydroids with short pelagic stages have nonetheless very wide geographic ranges, evidently the result of long-distance rafting.

Some fouling species may alternately raft as adults and disperse by means of plankton larvae, thereby achieving transport across wide reaches of open sea and across ocean basins. Such a phenomenon may be conceived as "hopping" between "mobile islands". However, drifting objects are relatively scarce at sea and the likelihood that a larva encounters such a "raft" is very small indeed (*vide*, Scheltema, 1971c).

To summarize, the ultimate distance that a species may

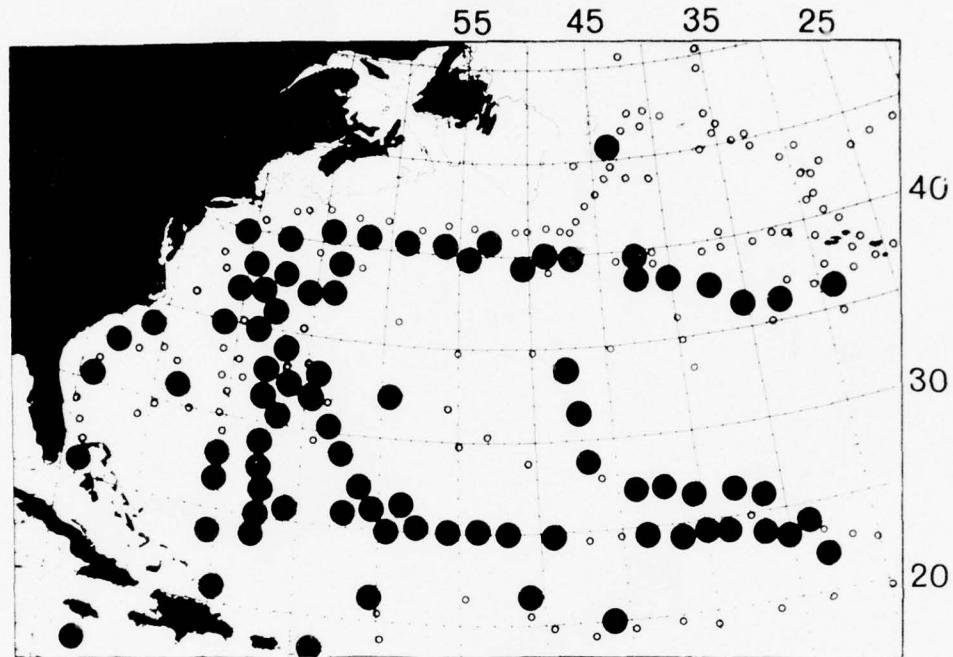


Fig. 1. Occurrence in the Western Atlantic and Sargasso Sea of cyphonautes larvae belonging to encrusting cheilostomous bryozoans. Most of the larvae are probably those of *Membranipora tuberculata* Busk commonly found on *Sargassum* weed. Large filled circles are locations where cyphonautes larvae were found in plankton tows. Small open circles are locations where cyphonautes were absent.



Fig. 2. Distribution of barnacle larvae observed in the North and Equatorial Atlantic Ocean. Larvae cannot be identified to species with certainty but belong mostly to the genus *Lepas* and *Conchoderma*. 1 - Locations where larvae were absent; 2 - locations where nauplius larvae occurred; 3 - locations where cyprid larvae occurred; 4 - locations where both nauplius and cyprid larvae occurred. Arrows indicate surface currents that suggest routes of dispersal. Eastward dispersal along the equator in the Equatorial Undercurrent or Lomonosov Current is not shown. The coastal origin of the cyprid larvae in the mid-Equatorial Atlantic is suggested by the absence of earlier nauplius stage larvae.

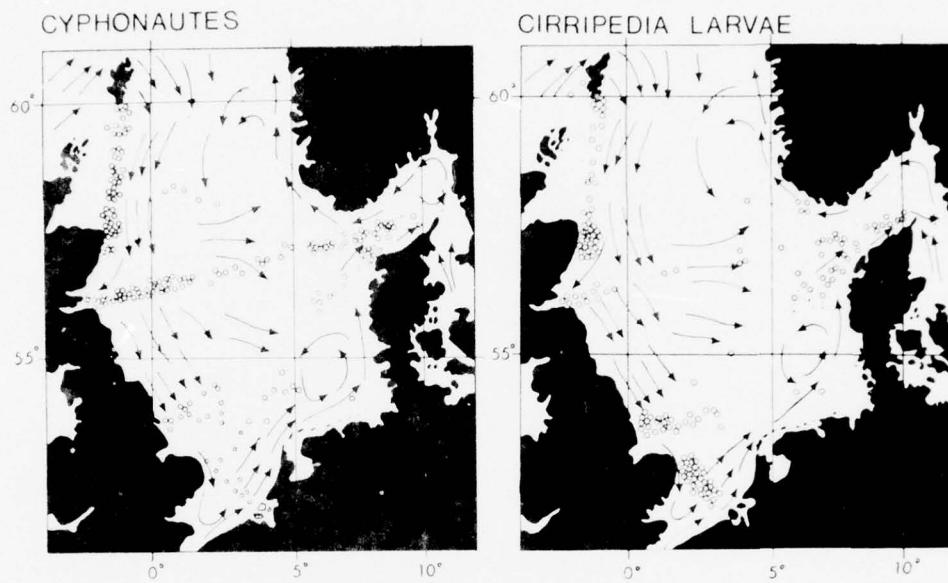


Fig. 3. Distribution of bryozoan and barnacle larvae in the North Sea. Nowhere do depths exceed 200 meters and in the area of the Dogger Bank depth is less than 50 meters. However, a deep trough that exceeds shelf depths of 200 meters extends from within the Baltic along the southern end and western coast of Norway. Each circle indicates the occurrence of larvae. Arrows show possible routes of dispersal by surface currents. (Modified and redrawn from Rees, 1954, p. 63.)

be rafted depends upon the ability of the adult to survive while afloat at sea. On the other hand, the distance that a teleplanic larva may be transported is directly related to the velocity of ocean currents and the ability of the larva to delay settlement. This latter subject, delay of settlement, has been considered elsewhere by Scheltema (1967, pp. 262-263) and by Doyle (1975).

Dispersal of larvae along the continental shelves and in near-shore waters has been observed mostly in temperate and boreal seas. Pelagic larval development of temperate species is ordinarily from two to six weeks (Thorson, 1961), but even in such a short time, a modest current of only 0.5 kilometers per hour can disperse a larva a distance of 150 to 500 kilometers.

Details of the circulation in coastal regions is always complex and seldom will a larva be carried directly between two points. Coastal currents may vary seasonally in both direction and velocity and these changes can affect the dispersal of larvae. Charts of the average circulation for each month of the year over the North American continental shelf between the St. Lawrence Estuary and southern Florida show striking seasonal changes in the surface currents between spring and late summer (Bumpus, 1973). In the region south of Cape Hatteras a complete reversal of the coastal surface circulation occurs in August, resulting in a strong continuous flow south from Cape Cod all the way to southern Florida.

The consequences of this temporal change in circulation is a seasonal difference in the direction and velocity of larval dispersal. Therefore, the time of spawning and the location of a parent population are relevant facts about a species which must be known to understand its dispersal.

Marked differences also exist in the direction and the velocity of currents at the surface and those just off the bottom (Bumpus, 1973). Over the continental shelf along the American seaboard the net flow along the bottom is always toward the shore. Hence the vertical disposition of larvae in this region is important in determining whether they will be transported out to sea or shoreward to the coast. Returns of drift-bottles and bottom-drifters show that the likelihood that a larva is retained in the coastal circulation increases from the edge of the continental-shelf shoreward to the coast and also is higher near the bottom than at the surface. Should the older larvae of species, by virtue of their behavior, tend to descend toward the sea floor, then the net transport of these late stages must be toward the coast. Thorson (1964) has shown through a review of the literature that a large percentage of late stage larvae are negatively phototropic and consequently will indeed be found deep in the vertical water column.

That the hydrographic mechanism described above can really act to retain larvae within the continental shelf region is suggested in a qualitative way by the very common occurrence of invertebrate larvae there (Nichols and Keney, 1963; Scheltema, unpublished data). Studies in other regions of the world show analogous hydrographic mechanisms must retain larvae near other coastlines (Knudsen, 1960; Makarov, 1969; Scheltema, unpublished data). Although the dispersal of larvae from fouling organisms has been little studied they are known to occur commonly in coastal regions.

Rees (1954) has plotted the distribution of bryozoan and barnacle larvae throughout the shallow waters of the North Sea. By superimposing the direction of the surface currents, it is seen that larvae can easily be carried along the entire coastline of this inland sea.

In order to understand the dispersal of pelagic larvae within and between estuaries, three important points need be considered: first, the number of larvae flushed out of the estuary; these larvae, although lost to the parent population, may help to extend the species range or establish gene-flow with neighboring estuaries. Second, the number of larvae retained within the estuary; these larvae upon settlement will help to maintain the endemic population. Third, the number of larvae entering the estuary but originating from some other region outside. These larvae will introduce new genetic variability and maintain genetic continuity with distant populations.

The loss of larvae by mortality and by transport out of an estuary was considered by Ketchum (1954) and Ayers (1956). By combining the equations for flushing of an estuary derived by Ketchum with the usual equation for mortality in populations, Ayers demonstrated that in a vertically homogeneous estuary with a high flushing rate, no possibility exists for endemic larvae to complete development, and all settlement within the estuary must come from immigrant, ready-to-settle larvae carried in with the flooding tide.

The retention of pelagic larvae has been studied in a number of coastal-plain estuaries where there is a net downstream movement of less saline water flowing out along the surface and a nontidal upstream drift of denser, more saline water moving up toward the head of the estuary along the bottom (Pritchard, 1955). Salt balance and volume continuity are maintained by gradual vertical mixing from the bottom to the surface stratum (Pritchard, 1952). The retention of barnacle larvae in a coastal-plain estuary was shown by Bousfield (1955) in the Miramichi in Canada. Plankton tows revealed that each successive nauplius stage lived deeper in the water column than its preceding instar. Consequently, whereas the early nauplii were transported

toward the mouth, the later stages, being below the level of no net motion, were dispersed upstream toward the head of the estuary. By the time that settlement became imminent most of the cyprids had been returned near the point of their parent populations. The retention of oyster larvae in the James River estuary was shown to result from a similar hydrographic mechanism, but complicated, according to Wood and Hargis (1971), by the fact that the veligers came off the bottom only during the flooding tide, thereby increasing the rate of their net upstream dispersal.

Because there is not yet a way to distinguish endemic from immigrant larvae, the introduction of new individuals from foreign origins has not yet been studied. Larvae near the bottom along the continental shelf of the eastern Atlantic seaboard will tend to be swept toward the coast and into the mouths of estuaries. From a knowledge of the abundance of larvae outside an estuary and from sea-bottom drifter data on the direction, rate and probability of shoreward drift, it is possible to approximate roughly the number of pelagic forms that should return shoreward or be entrained into estuaries. But the initial origin of such larvae will be unknown.

In order to understand the dispersal of larvae within an estuary system, the loss, retention, and entrainment of larvae need to be all considered simultaneously. This has not been done in any estuary.

In summary, all evidence indicates that larvae can effectively both maintain and extend species ranges. The importance of the larval dispersal on genetic exchange between populations will briefly be discussed in the following section.

THE RELATIONSHIP OF LARVAL DISPERSAL TO GENETICALLY-DETERMINED GEOGRAPHICAL VARIATION IN FOULING ORGANISMS

Until very recently, remarkably little study has been devoted to those factors which contribute to the geographical similarity and differences between marine invertebrate populations. Patterns of geographical variation may be disjunct, that is, with distinct differences between each spatially separated population, or they may be clinal showing gradients of change from one population to the next. Moreover, not all characteristics within a single species need vary geographically in a similar way, for example, certain attributes may show discrete differences between one population and the next, whereas others may be clinal or show no geographic variation at all.

Geographic variations between populations can be of two kinds: first, noninheritable adaptations resulting from

ecophenotypic responses of individuals within each population to the local environments (e.g., morphological adaptations and physiological acclimation, *vide*, Mayr, 1963, p. 140, Table 7-1). Since such variations do not directly affect succeeding generations, they need not be considered here. Second, genetically determined adaptations which are inherited from one generation to the next, and which according to contemporary theory will reflect (a) differences in the kind and intensity of natural selection that have occurred within each population, and (b) the effect of gene-flow that has taken place between the spatially separated populations. (In small or peripheral populations, genetic differences are said sometimes to result from "genetic drift" or the "founder effect".)

Selection in a stable and homogeneous environment is believed to reduce genetically determined variability, but there are other mechanisms known that tend to counteract this tendency (e.g., pleiotropy, the capacity of a gene to affect several characters at once, and epistasis, the interaction between non-allelic genes). New genetically determined variation in a population can arise from only two different sources. First, it can originate from spontaneous natural gene mutations. Second, and probably more commonly, it may be introduced by gene-flow or the exchange of genetic information between populations by means of pelagic larval dispersal. However, even when gene-flow by means of larvae is readily possible, genetic differences between populations may be nevertheless maintained as the result of local differences in the post-larval genotype favored by selection. There are a number of studies in which natural selection has been demonstrated to operate within a single generation in a remarkable way even though the species have moderately long pelagic developments of several weeks (Struhsaker, 1968; Koehn and Mitton, 1972; Levinton, 1973; Boyer, 1974). These studies (predominantly using electrophoretic techniques) suggest that natural selection was largely attributable to physical aspects of the environment.

The lack of genetically determined geographic variation is usually believed to indicate an unrestricted gene-flow throughout the species range. The seemingly remarkable similarity in gene-frequency between populations of the gastropod *Nassarius obsoletus* over a large portion of its range that was found by Gooch, *et al.*, (1972) was attributed by them to gene flow as a result of the dispersal of pelagic larvae.

Snyder and Gooch (1973) compared two species of intertidal gastropods (*Nassarius obsoletus* and *Littorina saxatilis*) and concluded that there exists "a strong correlation between population differentiation and dispersal ability". In a study of three species of *Littorina*, Berger

(1973) came essentially to the same conclusion. Populations of *Littorina littorea*, having a pelagic larval development, were genetically quite similar whereas populations of both *Littorina obtusata* and *Littorina saxatilis*, having non-pelagic development, differed markedly from one to the next.

These few examples are intended to show how natural selection and gene-flow by means of larval dispersal are both regarded as important in determining the amount of genetically-determined geographic variation and similarity in marine invertebrate species. The literature on population genetics of marine species has recently been usefully reviewed by Gooch (1975).

Genetically-determined variation has been presently studied in only very few species that can be regarded as fouling organisms (e.g. *Mytilus edulis*: Koehn and Mitton, 1972; Milkman *et al.*, 1972; and Boyer, 1974; the bryozoans *Schizoporella errata* and *Bugula stolonifera*: Gooch and Schopf, 1970). Yet many fouling organisms may be ideal for the study of such geographic variation. Because ecophenotypically determined morphological, physiological and behavioral characteristics may be fixed early during ontogeny, even in the face of environmental change (Kinne, 1962), it is in practice often quite difficult to distinguish between genetically and non-genetically determined variation. Therefore, only through laboratory breeding experiments can environmentally induced and genetically determined variation be unequivocally distinguished. Many fouling organisms are potential subjects for such breeding experiments since (1) they are relatively easy to breed in the laboratory, (2) possess short life cycles, (3) produce numerous offspring, and (4) have wide geographic distribution. The understanding of geographic variation in marine fouling organisms may have important consequences for their control. It cannot be assumed, for example, that a species will respond similarly throughout its geographic range either physiologically or in its settling responses (Knight-Jones, *et al.*, 1971; Doyle, 1975).

LARVAL SETTLEMENT AND HABITAT SELECTION IN FOULING ORGANISMS

The ability of a pelagic larva to choose a habitat for attachment is very important to its survival as an adult. Indeed, evidence accumulated during the past 50 years shows that settlement of sedentary species is not usually random but frequently quite selective. Larvae if given a choice often demonstrate a remarkably distinct preference for their site of attachment. (Settlement as used here is an ecological term referring to termination of pelagic larval

existence and assumption of a sessile or attached mode of life.) Both physical and biological attributes of a habitat may affect the settlement response.

Physical characters that affect settling are of two kinds: first, the surface properties of the substratum; and second, vector quantities such as currents, gravity and light.

Properties of submerged surfaces, such as texture, surface angle, and color affect the settlement behavior of barnacle cyprid larvae (Crisp and Barnes, 1954; Barnes, 1956). The calcareous tube worm *Hydroides*, an important fouling organism in warm-temperate and tropical seas, prefers rough surfaces for attachment, whereas the planula larva of the hydrozoan coelenterate *Tubularia larynx* is indifferent to surface texture. Some species, such as the American oyster *Crassostrea virginica*, seem actively to prefer smooth surfaces for settlement. No generality can apparently be made regarding the response of larvae to surface texture and different species appear to respond differently. Surface contour has been demonstrated to be an important factor in settlement of barnacles; cyprid larvae will settle in greatest abundance in the bottom of concavities or pits (Crisp and Barnes, 1954).

An understanding of the settlement responses to physical attributes of the environment can best be understood by observing larval behavior just before and during settlement. Such detailed observations have been made for the common boreal barnacle *Balanus balanoides*, the tube worm *Spirorbis spirorbis*, and the European oyster *Ostrea edulis*. An interpretation of the behavior of larvae should include a knowledge of the sensory receptors involved, but little is yet known about either the details of the morphology or functioning of such structures, although the microscopic anatomy at settlement for the above forms is now known. A thorough study of the sensory receptors of fouling organisms at the time of settlement should be of considerable practical value in devising means to prevent marine fouling.

The effect of water currents on settlement has been studied mostly for barnacle cyprids. The flow-rate at the potential attachment surface and its gradient with distance from such a surface are important to settlement (Crisp, 1974). However, the velocity gradient will also depend on the textural properties of the surface, e.g., roughness and contour. Barnacle cyprids do not attach at a very low velocity gradient; apparently an optimum gradient exists above and below which the likelihood of attachment diminishes. Since post-larvae depend upon currents for food, their orientation to current direction and velocity established at settlement is adaptive for survival.

It is often difficult from field studies alone to distinguish between the effects of light and gravity; for example, it may be impossible to separate negative phototropic responses from positive geotropic reactions or indeed from negative photokinesis and subsequent effects of gravity. The precise behavior of larvae must be known in order to interpret data from the natural environment. On the other hand, light conditions that occur in nature are difficult to simulate in the laboratory because of the refractive properties of the enclosed vessels that must be used. In a general way, however, field experiments suggest that most larvae prefer shaded areas for settlement and that they presumably avoid a direct light source at the time of settlement. The presence of statocysts in some larvae such as bivalves suggests that gravity may be important for the orientation of such species.

The literature on the effect of physical factors that influence settlement of marine larvae is usefully summarized by Crisp (1974); and Thorson (1964) has reviewed light as an ecological factor in the settlement of marine invertebrates.

The biological properties of an environment known to elicit settling responses in larvae of invertebrate fouling organisms may be readily placed into three general categories (Scheltema, in press). These are: (1) responses of a larva to the microflora of a filmed surface; (2) intra-specific or "gregarious" responses - the reaction of a larva to other members of its kind that are already settled; and (3) interspecific responses, the reaction of a larva to other invertebrate species with which it is usually associated as an attached adult.

A primary slime-film of bacteria and closely related microorganisms is formed when glass slides or any other smooth surfaces are immersed in the sea for twenty-four hours. ZoBell and Allen (1935) proposed that this film was a prerequisite for the later settlement of larger fouling organisms. Wood (1950) found the primary film in his experiments was not bacteria but rather "algal spores, diatoms, and amorphous organic material" and concluded that bacteria play only a secondary role in the formation of a primary film. The question arises whether the presence of a film is an obligatory step in ecological succession of an attached community (as proposed by ZoBell) or whether sedentary organisms could settle directly on newly submerged surfaces. This question was investigated experimentally in the laboratory by Miller, Rapean and Whedon (1948) using the bryozoan *Bugula neritana* and also in field studies of fouling plates by Scheer (1945). The results suggested that although slime films facilitated settlement of bryozoans, it was not a prerequisite.

Subsequently there has been considerable evidence both

from the laboratory and field observations that settlement of a wide variety of fouling organisms is promoted by the presence of slime films (e.g., Cole and Knight-Jones, 1949, *Ostrea edulis*; Knight-Jones, 1951, *Spirorbis borealis*; Wisely, 1958, the bryozoan *Watersipora cucullata*). The specific role of bacteria to settlement has been studied by Müller (1973) for *Hydractinia* in great detail. There remain some species, however, such as the hydroid *Tubularia larynx*, whose larvae are indifferent to the presence of a slime film.

There is evidence that the microfloral composition of the film may bear some relevance to its "attractiveness" for the settlement of fouling organisms. Meadows and Williams (1963) showed that primary films which had different algal components showed different degrees of attractiveness for the polychaete *Spirorbis borealis*.

Evidence for the preference of larvae to settle in close proximity to other already attached members of their own species (i.e., intraspecific or "aggregation" responses) comes largely from the study of oysters and barnacles. The earliest observations appear to be those of Cole and Knight-Jones (1949) who noticed that the total number of oyster larvae settling on surfaces from which newly settled post-larvae were daily removed was one-half to one-third as many as in controls from which post-larvae were not removed. Knight-Jones and Stevenson (1950) subsequently demonstrated that the settlement of the acorn barnacle *Elminius modestus* was much heavier on areas which already bore recently settled barnacles than on similar adjoining areas where barnacles were absent. It was concluded that this difference "was probably largely because of gregariousness". Additional research has now shown that the cyprid larvae of a number of other species (viz., *Balanus balanoides*, *B. crenatus*, *B. amphitrite*, *B. tintinnabulum* and *Chthamalus stellatus*) behave in a similar fashion, and that they tend to settle near populations of their own adults. Knight-Jones was able to show that the gregarious response was highly specific. *Balanus balanoides* cyprid larvae, for example, settled more readily with adults of their own than with those of other species. It appears, at least among some species (e.g., barnacles, serpulids) that if the pelagic life is too prolonged, discrimination of the larvae at settlement is greatly diminished; direct evidence on this point, however, is lacking for most species (Knight-Jones, 1953; Meadows, 1969).

The biological basis of gregarious response was examined in detail by Crisp and Meadows (1962) who treated inert surfaces with aqueous extracts of whole barnacles. Cyprids settled on such treated surfaces as readily as on surfaces bearing adult barnacles, thus simulating the gregarious settling response. The soluble settling factor proved to be non-dialyzable, heat stable in water and resistant to severe

physical and chemical treatments; the threshold of *B. balanoides* cyprids for extracts of their own adults was 0.08×10^{-2} mg protein ml⁻¹. Crisp and Meadows concluded that the attractive substance was a water-soluble fraction of arthropod cuticle and that the cyprid responds to a "specific molecular configuration manifested by the protein only when physically bound to a surface" and not by orienting to a chemical gradient. The most recent attempt to define the settling factor of barnacles has been by chemical, chromatographic and electrophoretic separation of partly purified extracts of *Balanus balanoides*. Gabbott and Larman (1971) found two active components, one probably a glycoprotein or mucopolysaccharide-protein complex, the other a protein associated with nucleic acid. Research on gregarious settlement in oysters has yielded results very similar to those obtained with barnacles (Crisp, 1967; Bayne, 1969; Hidu, 1969; Beitch and Hidu, 1971; Keck, et al., 1971).

More complex than intraspecific relationships are the interspecific associations found in fouling communities. That settlement responses might be important in initiating such relationships has had little consideration experimentally until quite recently.

Cole and Knight-Jones (1949) noticed that surfaces that had become heavily fouled with sessile organisms such as filamentous algae, ascidians, patches of bryozoa, calcareous tube-worms, hydroids, and small mussels had greater settlement of oyster larvae upon them (3099) than shells that were cleaned daily of all their fouling (833). The effect of gregarious settlement was avoided in the experiment by daily removing all settled oyster-spat.

Although larvae of oysters are seemingly "attracted" or "induced to settle" by the presence of a pre-existing fouling community, larvae of certain other species apparently can be inhibited. Hence, Goodbody (1961) noted that a mature colony dominated by sponges and sea anemones on a submerged panel inhibited the colonization in adjacent panels of a primary colony.

A few laboratory experiments have demonstrated interspecific settlement responses but most of these have not dealt with common fouling species. Bourdillon (1954) showed that planulae of the anthozoan *Alcyonium coralloides* preferred to settle on gorgonian corals and Birkland, Chia and Strathmann (1971) found that brachiolaria larvae of the common seastar *Mediaster aequalis* settled in response to tubes of the polychaete *Phyllochaetopterus*. In a few instances settlement of a predator has been experimentally related to the proximity of its prey. Hence, opisthobranchs often settle in response to the bryozoa on which they feed (Thompson, 1958).

The study of interspecific settlement responses among

fouling organisms has scarcely begun. To what extent the species composition of fouling communities is established by "settlement responses" and, on the other hand, to what extent by interspecific competition after settlement is a question which until now has been largely unanswered.

CONCLUSION

Marine fouling studies in the past have been largely empirical dealing principally with the efficacy of particular treatments for its prevention (Woods Hole Oceanographic Institution, 1952). However, adequate solutions to some of the problems of marine fouling require more precise biological information on individual species (e.g., morphology and physiology of sense receptors at the time of attachment; settlement responses and behavior at settlement; and genetically determined geographic variation in growth and settlement preferences). Only with such improved knowledge is it likely that new approaches to the control of marine fouling will present themselves.

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THE ORIGIN AND DISTRIBUTION OF EPIBIOSES
IN THE UPPER REGIONS OF THE SHELF OF THE NORTHWESTERN PART
OF THE PACIFIC AND THE POLAR BASIN

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To form a correct conception of the distribution regularities of marine ecosystems and of the quantitative apportionment of the living organic matter within them, one should have at his disposal a clear and dependable theory concerning the origin, formation and development of the corresponding biocenoses. Epibiosis (epifauna + macrophytes) has proven to be the most ancient, stable and productive layer of many biocenoses, determining their outward aspect and considerably influencing the composition and quantitative development of endobiosis (infauna). Epibioses are actually composed by almost all bottom autotrophs and the most ancient representatives phylogenetically of the majority of classes of marine invertebrates (Spongia, the majority of bottom Coelenterata, Bryozoa, Brachyopoda, representatives of plesiomorphous families - Phylodocidae and Aphroditidae of Polychaeta, the majority of the most primitive classes in each line of development of Crustacea, all the representatives of the originally more ancient subclasses of Cyclobranchia and Fissobranchia of Gastropoda, the major part of Tunicata, the relatively most primitive of bony fishes of the families Gonorhinchidae and Nothocanthidae).

Epibenthic organisms differ from animals inhabiting algae and the sea grass leaves, by their less developed morphological specialization, as well as from those which bury themselves in the ground. Epibioses, constituting the most ancient parts of ecosystems, are usually characterized by a high species diversity. Thus, in biocenoses of the Possjet Bay (Scarlato, Golikov *et al.*, 1967), the species diversity, measured according to Shannon-Weiner ($H=-\sum p_i \ln p_i$, where $p_i=N_i/n$), is, on the average, 1.2 for the epifauna, 1 for the fauna, and 0.9 for the phytal animals.

The maximum of species diversity in epifauna (1.86) can be observed in the bay at depths ranging from 1 to 5 meters

among rocks and stones. According to their feeding fashion in epibioses, the sestonophages are predominant on hard grounds, while on soft grounds and mixed grounds there are mostly detritophages and necrophages.

The majority of epibiotic representatives have the plankton phase of development in their ontogenesis, which is most typical for epibioses in warm and temperate waters.

The mentioned ontogenetic phase produces a considerable influence upon special distribution and the total number of individuals in specific populations, thus it should be considered an important part of the corresponding ecosystems. Besides, taking into account the biotopic attachment of the ecosystems to space and time factors, they are composed exclusively by sinking larvae and those dwelling in the water layer, which directly dispose above the corresponding epibiosis. A considerable part of the plankton larvae of macrobenthic organisms spreads beyond the ground habitation of the local populations and, as a temporary component, joins the ecosystems composed of other species.

Under favorable conditions, the plankton larvae of bottom organisms are slow in their development and if they have sunk to the bottom they usually finally perish.

A formation of mass populations of young *Mytilus edulis* and *Crassostrea gigas* gives a typical picture of the development and sinking of plankton larvae of bottom organisms under unfavorable conditions, which we have often enough observed within the littoral zone in districts influenced by mobile ice or by a strong and continual water freshening.

Mytilus edulis, which have sunk to the littoral in summer, experience some growth toward the autumn season and sometimes become the leading forms of the biocenosis.

In winter, however, influenced by mobile ice or by excessively low temperatures at ebb-tide, the populations of *Mytilus*, whose individuals have in general not yet reached maturity, are almost completely destroyed, while the representatives of the genera *Fucus*, *Littorina*, *Balanus* or *Chthamalus* begin to play the leading role in biocenoses.

The same may be observed with *Crassostrea gigas* in the Sea of Japan littoral and in the continually freshening shoal waters. The plankton larvae of these species are reproduced at the expense of sublittoral populations dwelling in favorable conditions.

As is well-known (Thorson, 1936, 1950; Mileikovsky, 1971; and others), many species of epibioses in cold water have a direct development, which is evidence of genotypic adaptation to existence under severe conditions with a very low content of feeding substance in the water mass during the greater part of the year.

Obviously, species following this type of reproduction have a less extensive distribution than those with a

plankton phase of development in their ontogenesis. Thus, a number of Pacific boreal species of bivalves, which have the plankton-larva phase in their ontogenesis, are spread far toward the north and reach the Dezhnev Cape and the Beaufort Sea, while, judging by the distribution of gastropods of *Neptunea* genus (Golikov, 1963), whose young individuals develop directly from bottom egg capsules, the northern border of the Pacific boreal district lies in the Bering Sea to the south of the Anadyr Bay and Norton Sound Bay. It is characteristic of mobile organisms (e.g. Amphipoda - Gurjanova, 1951, Tzvetkova, 1975; or fishes - Andriashev, 1939) that irrespective of their manner of reproduction, they have a somewhat larger distribution area than organisms with restricted mobility, devoid of a pelagic development stage. This is again striking evidence of the vital importance of the plankton-larva phase for the widest distribution of organisms (within the range of genotypic characteristics).

The formation of floro-faunal complexes and their further distribution, history, geography and evolution are reflected in the formation of epibioses of the upper regions of the shelf in the northwestern part of the Pacific and the Polar Basin. It is clear that local specific populations are elementary units, organizing the floro-faunal complexes and the ecosystems which they compose.

The process of speciation, consisting of a series of gradual eco-physiological adaptations, first on an organic level, then on tissue, cellular and molecular levels of organization, and changing from modificationary alterations to genotypical reorganization via selection at the molecular level (Golikov, 1973), must have preceded the process of distribution of local populations when conditions became greatly changed. The history of the fauna formation of separate groups of marine benthic animals (Golikov, 1963; Kafanov, 1974; Scarlato, Kafanov, 1975; Tzvetkova, 1975) gives some evidence of the fact that the process of species formation was induced by excessive changes in climate and by a further formation of corresponding water masses. A strict correlation between the speciation and the changes of the force and direction of physico-chemical factors, determining the properties and distribution areas of the newly formed genotypes, offers an opportunity to reconstruct in space and time the specific evolution of organisms even when their fossils are totally absent (Golikov, Tzvetkova, 1972).

The rearrangement of the interlocked DNA, RNA and protein synthesis and the change in primary structure and fermentation activity of proteins, corresponding to the changes which called forth speciation, must have occurred simultaneously and in the same way in every species inhabiting a certain area when they experienced the influence of the same factors inducing speciation. Besides, species of different

systematic groups have similarly changed their condition requirements, securing a successful replication of hereditary properties necessary for reproduction processes. Accordingly, the newly formed species of flora and fauna (including those belonging to different phylogenetic branches of floral and faunal development, and to different large taxons), having in common the time and place when and where they were formed, acquired quite comparable distribution possibilities. As a result, modern species, belonging to different phylogenetic subdivisions, have formed objective biogeographical groups. The distribution of such groups of species coincides with the areas of present-day biogeographical regions and often corresponds to the positions of definite water masses.

The formation and future distribution of species was closely connected with the position of the level of the World Ocean (Lindberg, 1948, 1955, 1974); its large geohydrodynamic variations have usually coincided with global climate changes and with changes in the thermal water regime. We have every reason to assume that stenobiotic species with a narrow tolerance range have been formed and have distributed themselves (simultaneously within phylogenetically differing species) during periods of ocean regression, while eurybiontic species with a considerable tolerance range were formed during periods of ocean transgression when the sea shoals with variable hydrological regime occupied vast areas of modern land (Golikov, 1974).

The history of the fauna formation of different systematic groups of organisms shows that the most powerful outbreaks of speciation took place at the time of climate-cooling. It is of interest to note that in cold and temperate waters, formed during the Cenozoic period when the temperature was falling, these large phylogenetic groups of organisms which had originated during the periods of planetary climate-cooling in the preceding geological epochs, attained the greatest quantitative development (Golikov, 1975). For instance, the late Carbonic-Permian catastrophic temperature minimum (which occurred about 250 million years ago) resulted in the formation of the first representatives of a series of systematic groups of a large taxonomic order (Peracarida isopoda, Amphipoda and others, a number of Bryozoa groups, Mollusca, etc.), whose descendants later in the Cenozoic period developed in vast quantities simultaneously in the cold and temperate waters of both hemispheres. In the ecosystems of tropical and subtropical waters, however, any existing representatives of the same groups have formed very small biomasses. This phenomenon may be accounted for by the formation of special enzymes which come into existence at low temperatures and constitute the basis of certain phylogenetic lines of species formation. These enzymes

are most active in the descendants of those species in cold waters, since they undergo a genetic suppression at relatively high temperatures.

One can suppose that species of epibioses, which first experienced the direct influence of changing condition factors, rearranged themselves at a quicker rate than infauna species, which have, to a certain extent, been protected by the micro-conditions of the ground.

The formation of epibioses, constituting the living basis of the ecosystems, followed the formation of biogeographic groups adequate to the environment; they were formed through co-adaptation and integration of local populations of species with similar environmental requirements. Species with different morphofunctional and physiological properties formed populations on different types of ground and at different depths, arranging themselves in interchanging layers which were sometimes of considerable extent.

As a rule, the process of epibiosis formation on ground devoid of living organisms begins with the settling of small and primitive organisms (a bacterial pellicle, meiobenthic organisms followed by algal growth, or spongia and hydroid growth). Then, depending upon the surrounding physico-chemical and biotopic environment, in the presence of biologic overgrowth already formed, larvae predominantly of Cirripedia, Gastropoda, Bivalvia and Polychaeta of the families Serpulidae or Sabellidae, begin sinking toward the biotope.

In the majority of cases, species populations of sufficiently larger size and weight which form the biological background of the whole biotope play the dominant part in epibioses, when after a temporary succession they enter the climax state. Besides, the optimum of biological functions in populations is attained by each species under conditions similar to those of their primary adaptation, timed to the formation of their genetic fund.

Background-forming species at certain depths in optimal conditions (for their genetic fund) acquire their greatest energetic power and form the basis for corresponding ecosystems, while other organisms join through co-adaptation with the leading forms, or by entering still unoccupied ecological niches. For example, in the Sea of Japan the background forming species of bivalves, *Crenomytilus grayanus*, has the highest population density and the heaviest biomass (up to 40 kg/m²) in the Bay of Peter the Great at a depth of 2-12 (sometimes 20) meters; at such depths they often form solid aggregations and become the leading forms in epibioses, not only on rocky grounds, but also sometimes on silted grounds.

In the Tartar Bay, where the water temperature in summer is, on the average, lower than the optimal temperature for this species, *C. grayanus* is rarely found and yields the

leading part in ecosystems to other organisms. Another background-forming, more warm water species, *Crassostrea gigas*, forms ecosystems in the western part of the Sea of Japan exclusively in well-protected bays, which are sunwarmed in the summer, and is totally absent along open coasts. *C. gigas* may have spread themselves toward the north and penetrated into remote, well-protected districts during periods of climate-warming in former geological epochs (Golikov, Scarlato, 1967; and others). As the background-forming species often find favorable reproduction and development conditions in districts of water areas remote from each other, one can often observe a certain interzonation in the distribution of ecosystems which is also reflected in the biogeographical aquatoria regioning (Golikov, Scarlato, 1968; and others). In epibioses with leading background-forming species, the total number of species, population density and biomass are considerably higher than in biocenoses where the leading role is played by species which offer no refuge or feeding material for other animals (Figs. 1, 2).

Here, in brief, is the history of the formation of biogeographical floro-faunal complexes in cold and temperate waters of the northern hemisphere and the history of modern epibioses formation on the basis of the former.

Figure 3 shows conjectural centers of origin of floro-faunal complexes, and the ancient and modern ways of distribution of the species composing them. When retracing the formation of complexes, the authors used the ecological principle of evolutional constructions on the basis of a knowledge of ecology and the distribution of recent biogeographic groups of animals (Golikov, Tzvetkova, 1972).

Data on paleofloras and paleofaunas allow us to imagine more or less clearly the pattern of climatic changes in the northern hemisphere during the last geological epochs. Paleogeography of the northern hemisphere is also well-known. The paleogeographic pattern of the recent geological past can be successfully restored by analyses of the geographical distribution of recent species. We can consider as an example the reconstruction of the Quartenary geological history by means of the biogeographical method (Lindberg, 1955, 1972).

Application of the ecological method is based upon the very close dependence of the development of recent floras and faunas upon the history of climatic changes in any part of the Earth. This dependence is determined by the decisive influence of physical-chemical factors on processes of speciation and formation of faunas and also on their subsequent dispersal. Therefore, the juxtaposition of ecological data (first of all, those on thermopathy) and data on the distribution of recent species with information on climatic

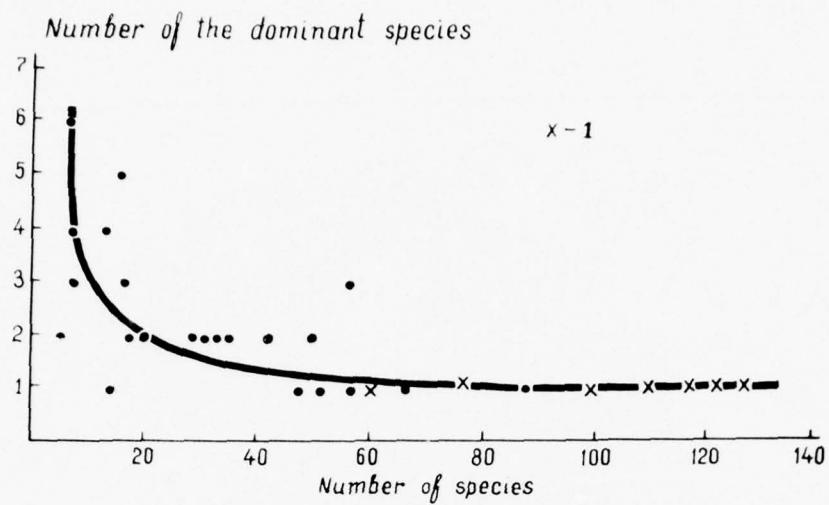


Fig. 1. The general number of species in biocenoses versus the number of leading species and the presence or absence of background-forming species (1) in the Possjet Bay, Sea of Japan. The ordinate value corresponds to the number of leading species in a biocenosis; the abscissa value shows the general number of species.

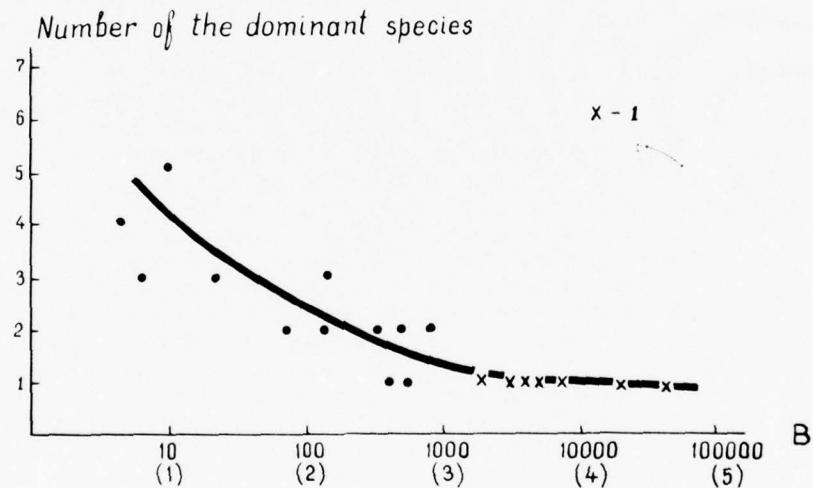


Fig. 2. The general biomass in biocenoses versus the number of leading species and the presence or absence of background-forming species (1). The ordinate value shows the number of leading species in a biocenosis; the abscissa shows the biomass (B) in g/m^2 in a logarithmic scale.

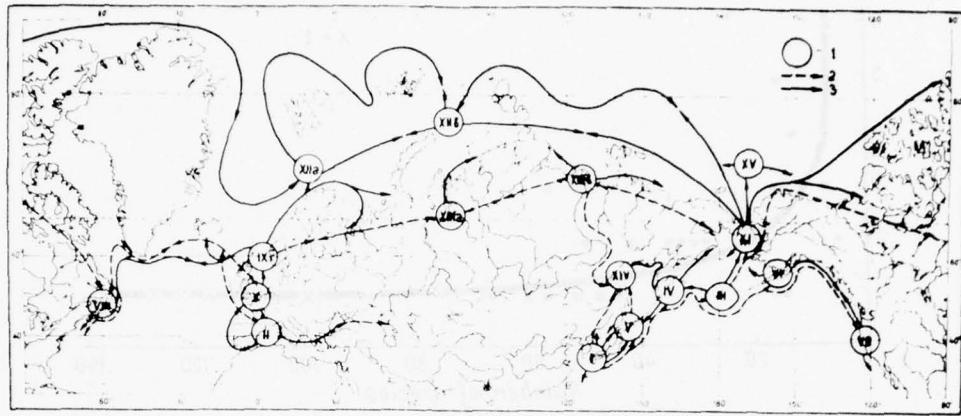


Fig. 3. Centers of origin (1), the ancient (2) and modern (3) distribution pathways of different biogeographical floro-faunal complexes of species in cold and temperate waters of the northern hemisphere as related to geohydrocratic alterations of the ocean level in different geological epochs. I - Pacific Asiatic subtropical species (early Miocene, regression). II - Mediterranean-Lusitanian subtropical species (early Miocene, regression). III - Pacific widely distributed boreal species (middle Miocene, beginning of transgression). IV - Pacific Asiatic widely distributed species (late Miocene, beginning of regression) and Pacific high boreal species (middle Miocene, beginning of transgression). V - Pacific Asiatic low boreal species (early Pliocene, regression). VI - Pacific American widely distributed boreal species (late Miocene, beginning of regression). VII - Pacific American low boreal species (early Pliocene, regression). VIII - Atlantic widely distributed boreal species (late Pliocene, transgression), and Atlantic high boreal species (late Pliocene, transgression). IX - European widely distributed boreal species (middle Pliocene, transgression) and European high boreal species (Pleistocene, next to last transgression). X - European low boreal species (late Pliocene, transgression). XI - Boreal arctic species, Pacific by origin (late Pliocene, transgression). XII a,b - Arctic and west arctic widely distributed species (early Pleistocene, regression). XIII a,b - Estuarine arctic species (Pleistocene, transgression). XIV - Glacial Okhotsk Sea Species (Pleistocene, ultimate stage of regression). XV - East arctic species (Pleistocene, regression).

and paleogeographic history allows us to imagine an ecological environment which was inhabited by these species in the past and to trace ways of their possible distribution. This analysis also allows us to achieve some idea of the probable time and place of origin of the species in question.

Subtropical by origin and subtropical-boreal by area, character species which originated during the beginning of the Miocene (about 25 million years ago) in the region where the Japan Islands are now situated are the most ancient components of modern ecosystems (I).

The low level of the ocean at that time and the absence of strict hydrological borders between waters washing the coasts of Asia at latitudes from Japan to the Bering land might have stimulated a wide distribution of these species. After further climatic cooling, these species disappeared from aquatoria with unsuitable temperature regimes, but survived and until the present were dominant in epibioses in protected bays of the Sea of Japan, the southern part of the Okhotsk Sea, northern Japan and the southern Kuril Islands, which are well-warmed in summer. *Littorina brevicula* in the littoral and species of *Sargassum* genera, *Crassostrea gigas* and some others in the shoals and sublittoral are examples of such species.

At the same time or at a somewhat later period, in the remnant of the Tetis Sea, the Atlantic subtropical species (II) were being formed; some of them later spread toward low boreal waters and composed the shoal ecosystems along the coasts of France, England and Germany.

The temperature drop during the second half of the Miocene (15 to 20 million years ago) resulted in the formation of the corresponding widely spread boreal Pacific species; a considerable part of them hold the leading role at present in the epibioses of the shelf and bathyal on both the Asian and American coasts of the Pacific, or are parts of ecosystems with other dominant species. The formation of these species might have taken place in the southern part of the Bering Sea (III), while their wide distribution may be accounted for by the comparatively equal hydrological conditions in the Pacific up to the latitude of 38-39° N at the middle of the Miocene. Later, when the water regime of the northern and southern parts of this aquatorium became strictly different, these species either changed their reproduction periods or survived at considerable depths. *Fucus evanescens*, *Chthamalus dalli*, *Mytilus edulis*, *Littorina kurila*, *Metridium senile fimbriatum* and others may serve as examples of species in this biogeographical group, playing the leading role in epibioses and forming species associations.

In the Sea of Japan, widely distributed boreal Pacific species form intermittent associations only on open coasts

in relatively cool waters, while further to the north they are more commonly the leading forms in epibioses in protected districts.

The growth of a difference in the hydrological regime of Asian and American coastal waters and the great depths which were formed in the southwestern part of the Bering Sea caused a differentiation within Asian and American coastal boreal species, which were formed correspondingly at either Kamchatka (IV) or Alaskan coasts (VI).

Some of these species are, at present, the leading forms of a series of shoal epibioses (*Gloiopektis capillaris*, *Zostera asiatica*, *Collisella digitalis*, etc.), while others have formed common secondary components of ecosystems with dominant species of a different genesis.

In the late Miocene (about 10 million years ago) due to the progressive decrease in temperature, a large difference in newly-formed hydrological conditions established a border between the upper boreal and lower boreal waters of the Pacific, which caused, at the very end of the Miocene or at the beginning of the Pliocene, the formation of high boreal Pacific species at the southeastern Kamchatka coasts (IV) and the formation of Asian low boreal species at the point where Southern Sakhalin and Hokkaido are presently situated (V).

At approximately the same time, coastal American low boreal species sprang into existence along northern California (VII). Due to their unequal genotypical tolerance, caused by conditions under which they originated, high boreal and low boreal species were unable to spread themselves beyond the borders of the corresponding sub-regions. In epibioses of the shelf in the coastal Asian low boreal waters, such background-forming species as *Laminaria japonica*, *L. cichorioides*, *Crenomytilus grayanus*, *Modiolus difficilis* and others are usually the dominant species, while in high boreal waters the leading role is played by *Alaria fistulosa*, *Podenus macrochisma*, *Chlamis beringianus*, *Balanus cariosus* and others.

A mighty ocean transgression in the second half of the Pliocene caused a series of eurybiontic representatives of the boreal Pacific flora and fauna to migrate through the northern part of Canada, which was covered with water, toward the North Atlantic. At that time, the boreal hydrological regime established itself in the North Atlantic and an original boreal Atlantic species was formed. It was predominantly composed of immigrants from the Pacific, re-formed into peculiar species (more seldom into subspecies) on the coasts of America (VIII) or Europe (IX, X). The smaller part of the species was formed along the coasts of Europe from local *Tetis* and *Paratetis* genetic elements (species of *Gammarus* genera, *Tritia* and others).

Representatives of *Fucus*, *Laminaria*, *Littorina* and other genera dominate in epibioses of the shoals in many parts of the Atlantic boreal region.

A considerable progressive cooling toward the end of the Pliocene (2.5-3 million years ago), which resulted in the formation of glaciers in Greenland, Iceland and the Bering Sea Islands (Einarsson, Hopkins, Doell, 1967; and others) and in a considerable drop in water temperature, must have put an end to the migration of the relatively warm water boreal fauna from the Pacific to the Atlantic. Between the Pliocene and the Pleistocene, the progressive temperature drop led to the formation of boreal arctic species in the northern part of the Bering Sea, which were Pacific by origin (XI), and in the Barents Sea, which were Atlantic by origin (XII). These species had an opportunity to distribute themselves widely across the whole Arctic Ocean; in relatively cool elitoral waters they joined the boreal epibioses of the Pacific and, to a lesser degree, of the Atlantic Ocean. Separate representatives of *Eunephthya*, *Musculus*, *Neptunea*, *Buccinum* genera and others dominate in a series of epibioses in arctic and high boreal waters.

The regression of the ocean, which started at the beginning of the Pleistocene (1.8-1 million years ago) strictly diminished the entrance of the North Atlantic warm stream to the coasts of northern Europe. This may have been the most important cause of the extensive freezing in the high Atlantic coastal latitudes during the Pleistocene. The hypothetical Thule mountain ridge that may have connected America, Greenland, Iceland and Europe at the point where northern England and western Norway are now situated, and which supposedly towered above the water, might have formed an unsurpassable barrier for the Gulfstream.

However, a dryland bridge between Europe and America, which appeared more than once, could only have occurred at a time when the ocean was regressing more excessively in the Neogene than many authors believed.

Such geological data as the fall in depth and the hollow formation in the early Pleistocene in many regions of the World Ocean (probably including the depths of the Polar Basin) and the formation of the basins, capable of containing vast water masses, as well as paleontological data (Saks, 1953; Kotenov, 1970; and others) offer a possibility for the hypothesis that the ocean level during this period was 500 meters lower than the modern ocean level.

The increase of freezing in the Polar Basin and the formation of the high arctic water mass with temperatures under zero during the whole year resulted in the formation of the arctic species in this basin; they are endemic in the Polar region, but originated from surviving boreal arctic species. Biogeographical and paleontological data (Saks,

1948; Gurjanova, 1957, 1970; Tolmachev, Turtzev, 1970; Golikov et al., 1974; and others) give evidence of the fact that at the time of the early Pleistocene regression the Arctic Ocean at the point of the Novosibirsky Islands was divided by the Lomonosov Ridge towering over the water. As a result, one part of the arctic species originated in the western part of the Polar Basin (XII), and the other, in the eastern part (XV). In the majority of arctic epibioses, arctic species do not form large biomasses and yield the leading role to the boreal arctic species. However, in some epibioses occurring in upper arctic waters, such species as *Laminaria longicruris*, *Anonyx sarsi*, *Strongylocentrotus golikovi*, *Buccinum hydrophanum*, *Oenopota gigantea* and others occupy the dominant position.

The arctic glacial Okhotsk Sea Species (XIV) may have originated toward the end of the mentioned ocean regression, in the hollow of the western part of the Okhotsk Sea formed at that time. Furthermore, these species have not developed and distributed to a great degree and in spite of their considerable diversity, they occupy only a subordinate place in the greater part of the Okhotsk Sea epibioses.

During the period of the next to the last transgression, which followed the early Pleistocene regression, when water covered the low-lying lands of Europe, Siberia and America, an estuarine arctic water mass was formed in the region where the upper arctic marine waters and the still warmer river waters were commingling, thus inducing the formation of the corresponding faunal complex (Golikov et al., 1974). Due both to the considerably eurybionthic character of the estuarine arctic species and to the existence of broad migratory paths among estuarine systems of Eurasian reservoirs during the next to the last transgression (Lindberg, 1970), which occurred about 100 thousand years ago, many of these species have an interzonal distribution. Species of the *Mesidothea* genera dominate in estuarine arctic ecosystems while in infauna, the bivalve molluscs of the *Portlandia* genus are predominant.

The subsequent less striking climate and ocean level changes and the gradual establishment of present conditions brought to life the present correlation between the biomass and biogenetic resources in species of different origin within epibioses.

It is a fact of certain interest that in the northern hemisphere one can observe a general tendency of development and distribution of the organic world from the southwest toward the northeast. This regularity is probably determined by the direction of the Earth's rotation and conforms with geomorphological changes and with the direction of movement of magma masses and sea streams.

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SEASONAL VARIATION OF CRAB LARVAE
ALONG THE OREGON COAST

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Bimonthly plankton samples were collected for two years along a transect off the central Oregon continental shelf ($44^{\circ}39'N$) to document the species of crab larvae present, their seasonality, and their onshore-offshore distribution in relation to seasonal changes in oceanographic conditions. During the fall and winter, surface currents along the Oregon coast typically flow northward with an onshore component. However, during the spring and summer, the surface flow is southward with an offshore component. Marked differences in oceanic regimes are associated with the current reversals.

The distribution of crab larvae off the Oregon coast is in general agreement with the known distribution of the adults, and to a lesser extent with the seasonal changes in ocean currents. Most larvae of the 41 identified species appear in the plankton from February through July within 18 km of shore with greatest abundance in May-June. The most abundant larvae are those of the intertidal and sublittoral species (*Pachycheles pubescens*, *Fabia subquadrata*, *Pinnixa littoralis*, *Cancer oregonensis*, *Pugettia* spp., *Pagurus granosimanus*, and *Pagurus ochotensis*) reaching densities of 10-1000 per m^3 at 2 and 5 km of shore.

The offshore or onshore transport of the larvae is relative to the intensity of coastal upwelling or downwelling; however, the extent of this transport generally is limited to within 18 km of shore. The differential behavior of larvae during their development is an important feature in determining their position in the water column and subsequent transport by coastal currents. Most early stage crab larvae are found near the surface, whereas late stage larvae are found deeper, near the bottom. Those few nearshore species (*Cancer oregonensis*, *Cancer magister*, *Pugettia* spp., *Lophopanopeus bellus*, *Emerita analoga*), whose larvae consistently occur offshore beyond 18 km, usually have a combination of the following features:

(1) their larvae occur in comparatively high densities during late spring and summer, (2) they have a relatively long pelagic life, and (3) their larvae may exhibit a strong photopositive response during the early megalops stage and occur in the surface waters. This "anomalous" behavior appears to be an adaptive feature enabling the early megalops of these species to be concentrated near shore by the onshore surface currents prior to settlement. Within 5-9 km of the coast, a strong onshore component of the surface currents coupled to a lesser degree with the conservative effect of alongshore tidal oscillations is believed to be the major mechanism retaining larvae in the vicinity of the nearshore parent populations, regardless of the season.

EXPERIMENTS ON THE DYNAMICS OF DEEP OCEAN
ECOSYSTEMS: ENERGY FLOW AND MASS FLUX

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The Departments of Biology and Chemistry at the Woods Hole Oceanographic Institution are involved in an integrated, interdisciplinary investigation of the energetic pathways of organic matter across the benthic boundary layer of the deep-sea off the east coast of the United States. Experiments and sampling are being conducted primarily at two permanent bottom stations (1800 and 3600 meters depth) using the manipulative and observational capabilities of the Deep Submergence Research Vessel ALVIN.

Surface-ship sampling for the past century in the deep-sea has allowed us to define the standing crop and community structure of the fauna at the sediment-water interface, but little is known of the functional significance of the biota in energy flow and remineralization processes.

In situ manipulative and observational capabilities with DSRV ALVIN are allowing WHOI ecologists to conduct long-term experiments and monitoring which will elucidate the pathways and the rates at which organic matter is converted to energy or biomass. The experiments and sampling include measurement of sedimentation rates using large traps, *in situ* oxygen demand and inorganic nutrient fluxes in the sediments using bell jar-like incubation chambers, *in situ* respiration and excretion on individual animals captured with traps and slurp guns, microbial degradation studies, colonization and succession on azoic sediment surfaces, growth studies using isotope aging techniques and feeding experiments using baits and time-lapse photography. The goal of the project is the ability to predict how variations in the rates and forms of organic matter input into the deep-sea affect community structure and remineralization potentials.

FOULING COMMUNITIES AND GENETIC DIVERSIFICATION
IN THE MARINE ENVIRONMENT

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'Fouling' communities share with other associations of marine organisms the property of undergoing qualitative and quantitative modifications, both in time and space. For research leading to the comparative analysis of the species present, of their settlement and growth periods, of populations succession, and of the abundance of the main sessile organisms in habitats exhibiting different features, the marine biologist may utilize artificial substrates immersed in the sea at various depths, in adequately pre-selected localities.

The use of these artificial substrates, and the possibility of situating them wherever required and for whatever length of time, permits one to carry on important 'natural' experiments useful for the solution of a wide range of problems in theoretical as well as in applied marine biology. The use of such procedures will provide an advantage to the marine ecologist wishing, for instance, to approach the question of the origin and evolution of benthic communities; to the biologist who wants to analyze the complex mutualistic and competitive interactions among the community members and to detect the nature of chemical mediators likely to play a fundamental role in these interrelations; to the student of larval biology and life histories; to the pollution expert, intending to utilize 'fouling' communities as indicators of water quality; and, finally, to the population geneticist trying to detect sympatric or allopatric intraspecific divergencies and to estimate the role played by natural selection in determining the observed

differences. The latter point is the one to which, as a geneticist, I will devote more attention. We shall see later how the results of research along the lines briefly listed above may, in turn, help the specialist in fouling communities to solve some of his particular problems.

In order to deal with evolutionary problems a preliminary illustration of the tools currently available to the ecological-geneticist might be useful: in other words, an illustration of what benthic organisms are suitable for the genetic analysis of differentiation.

The genetic basis for differences within and between geographically separated populations of single species has been studied through laboratory experimentation for very few organisms. The beginning of this area of research is marked by the discovery of species exhibiting visible genetic polymorphisms and, at the same time, suited for culture and crossbreeding in the laboratory. From this viewpoint some Isopods such as *Jaera* and *Sphaeroma*, copepods of the genus *Tisbe*, the compound ascidian *Botryllus*, and the polychaete worm *Pomatoceros* proved quite useful. As an example, I shall briefly refer to the case of *Sphaeroma serratum*, which is represented along the coasts of Brittany by five main morphs distinguishable by their color patterns. Bocquet, Levi and Teissier (see Lejuez, 1974, for reference) have shown that the phenotypes *discretum*, *tunulatum*, *ornatum*, *signatum*, and *albicans* are under the control of four pairs of independent alleles which make an epistatic series. The frequencies of these genes, although remarkably stable in time, vary from station to station. For a few years the geographic distribution of the species, in its various genotypes and phenotypes, has been followed with great interest. Some observations suggest a certain correlation of the frequency of the various morphs with temperature. It has also been possible to determine that the differences between localities are due to Wright effect since the density of natural populations of *Sphaeroma* is quite high. More recently, West (1964) and Bishop (1969) have carried out similar investigations in another species, *Sphaeroma rugicauda* which is very common along the English coasts. Here the morphs are controlled by several non-epistatically interacting genes. One of them, *yellow*, undergoes seasonal fluctuations with the highest frequency in winter, indirectly suggesting an adaptive function for this polymorphism.

Another example is offered by the colonial ascidian, *Botryllus schlosseri*, studied in Italy by Sabbadin (1972) and in the United States by Milkman (1967). For the population from the lagoon of Venice, Sabbadin and coworkers were able to discover the Mendelian basis of the color polymorphism characteristic of the species: segregation

at four loci accounts for orange, reddish and blue pigment cells, and singly or double-banded intersiphonal bands. But, as in *Sphaeroma*, the selective significance of the polychromatism in *Botryllus* can only be suspected.

A species where it has been possible to demonstrate the adaptive function of polymorphism, is the harpacticoid copepod *Tisbe reticulata*, characterized by a striking polymorphism consisting of the different distribution and color of pigment in the hypodermal cells of the cephalothorax and the free thoracic segments. In the lagoon of Venice the species is represented by three main forms which can be identified in both sexes, plus one minor variant. This polymorphism, controlled by a series of alleles at the same locus, v^V , v^M , and v is adaptive and balanced, being maintained by the superiority of heterozygous genotypes (Battaglia, 1964; 1970). In fact, we have experimental evidence that certain physical ecological parameters, such as salinity and temperature, act as powerful selective agents on the various genotypes. In particular, differences in the water temperature are responsible for differences in the equilibrium frequencies of the genes which control polymorphism, and this applies both to natural and experimental populations.

The possibility that the physical factors of selection also operate in another species of *Tisbe*, *T. holothuriae*, is indirectly suggested by the finding of different degrees of "concealed genetic variability" in populations from southern France living in marine and in brackish-water habitats (Battaglia, 1970). A similar situation which legitimates the hypothesis that these inter-population differences are due to different ecological characters, and consequently to different selective pressures of the environments from which the populations come, has recently been found in 2 populations of the upper Adriatic.

Moreover, the species *Tisbe holothuriae* shows varying tolerance to low salinities. The physiological geographic races are clearly genetic races, since the observed physiological differences are preserved in populations cultivated in the laboratory for years (Battaglia, 1967).

Another species, *Tisbe clodiensis*, exhibits a polychromatism which is controlled by only two alleles of the same gene. In this case polymorphism is balanced since heterosis plays an important role in its maintenance. The fact that in experimental populations of *T. clodiensis* equilibria are eventually reached suggests that this polymorphism has an adaptive meaning. However, the equilibrium values seem to depend to a considerable extent on the initial composition of the population, whereas the effect of factors such as salinity or temperature is less appreciable. In other words, in *Tisbe clodiensis* the more effective

factors of selection seem to be biotic rather than physical. An experiment has been devised to test the hypothesis that the genetic structure of populations of a marine species may be influenced by the biotic factors of the environment. The experiment consisted of raising in the same culture vessel two species of *Tisbe*, namely *T. clodiensis* and *T. reticulata*, both polymorphic and therefore suitable for visible manifestation of possible genetic effects of co-existence. It was found that whereas in *T. reticulata* the gene frequencies at equilibrium seem to be unaffected by the presence of *T. clodiensis*, the equilibrium values in the latter differ significantly according to the presence or absence of *T. reticulata* in the same culture vessel (Table 1). The mechanisms responsible for this phenomenon are still obscure, although it is likely that interactions of a chemical nature are involved between the two competing species.

As we have seen, the use of species exhibiting visible polymorphism is very effective for the study of evolutionary events over the short time intervals accessible to the biologist. But when this favourable condition is not available, another valuable method for revealing and estimating genetic variability is provided by the analysis of protein variation by means of electrophoretic techniques. Examples of this kind of investigation on marine populations are becoming more and more numerous. The main purpose is to elucidate the possible adaptive significance of these biochemical polymorphisms, and to see to what extent the observed genetic variability can be related to ecological stability or diversity.

Since this subject will soon be developed by Dr. Gooch and Dr. Levinton, who have devoted most of their recent research to biochemical polymorphisms of organisms belonging to fouling communities (see, for reference, Gooch, 1975; Koehn and Mitton, 1972; Levinton and Fundiller, 1975), I shall confine myself to reporting on a case of adaptive enzyme polymorphism recently investigated in our laboratory. The marine amphipod, *Gammarus insensibilis*, has been tested by electrophoresis for several enzyme systems. In particular, the esterase systems appeared polymorphic at the level of five loci (Battaglia and Bisol, 1975). The results of crosses and the agreement with the Hardy-Weinberg distribution indicate the genetic nature of this polymorphism. One of the loci involved, Est-6, undergoes wide seasonal fluctuations (Table 2) with deviations from Hardy-Weinberg due to an excess of heterozygotes. The observed changes in gene frequency seem to depend largely on natural selection. As also suggested by laboratory experiments, temperature must be the major factor in this respect.

Table 1.

Biotic factors of selection in *Tisbe clodiensis*. Frequency of the allele p in experimental populations of *T. clodiensis*, with and without *T. reticulata* in the same culture. Initial frequency = .50 (from Battaglia, 1970).

Sampling (every 20 days)	Monospecific populations	<i>T. clodiensis</i> + <i>T. reticulata</i>
1	.88	.59
2	.86	.69
3	.84	.49
4	.81	.60
5	.75	.65
6	.76	.69
7	.81	.65
8	.78	.61

Table 2.

Adaptive polymorphism in *Gammarus insensibilis*. Seasonal changes of gene frequency for the Est-6 locus (from Battaglia and Bisol, 1975).

Month	N	Gene frequency Est-6 - p
October	179	.10
November	140	.22
December	174	.45
January	119	.49
April	58	.21
May	38	.04
July	51	.02

As we have seen, copepods of the genus *Tisbe* provide very good material for population genetics studies in the marine environment. In addition to that, the recent discovery of several sympatric and allopatric sibling species, and of variable degrees of reproductive isolation in geographic populations of the same species make *Tisbe* an excellent organism for research on speciation patterns as well (Volkmann-Rocco, 1971; Volkmann-Rocco and Battaglia, 1972; Battaglia and Volkmann-Rocco, 1973).

There are species, such as *Tisbe holothuriae*, whose various geographic populations, including those separated by the Atlantic Ocean, are perfectly interfertile, with F_1 hybrids which are often heterotic. Populations of other species, like *Tisbe reticulata*, are interfertile but there is evidence of an incipient reproductive isolation. The most interesting case concerns *Tisbe clodiensis*, whose different geographic populations exhibit all stages of reproductive divergence ranging from complete interfertility to complete intersterility, with the frequent occurrence of "relative intraspecific incompatibility". A detailed account of this situation which in many respects resembles the case of *Drosophila paulistorum*, is in course of publication (Volkmann, Battaglia and Varotto).

Tisbe is now also the object of research on biochemical polymorphisms. The first results of electrophoretic investigations carried out for general proteins and fifteen enzyme systems in several species, races, and genotypes, show that the biochemical similarity increases with the degree of taxonomic affinity (Table 3).

The cases just described indicate the usefulness and relevance to the geneticist of some species belonging to the 'fouling' community or closely associated with it.

Both the discovery of easily reared benthic species, and the increasing application of electrophoretic analysis, have disclosed new perspectives to the study of genetic diversification in the marine habitat. We shall see now to what extent the results thus achieved may help the marine ecologist or the biological oceanographer to solve some of his problems. For instance, the demonstration of the selective importance of certain biotic environmental factors may lead to a new way of approaching the problem of the origin and evolution of benthic communities. This problem will be more adequately dealt with if, in addition to the genetic research, other kinds of studies are conducted aiming to detect the nature and function of possible chemical mediators. In the final analysis these mediators represent effects, far from negligible, of genic action. This approach will contribute to a better understanding of the adaptive and evolutionary strategies utilized by the organisms living in the sea.

The results of genetic studies conducted on fouling species can also help to elucidate some problems of larval biology with special concern to the question of inter-relations between larval and adult stages. Perhaps the consideration of biotic factors of selection will provide a useful background for a further discussion of this interesting point.

We have already seen how, in *Tisbe clodiensis*, unlike *T. reticulata*, biotic factors appear to play a far more significant selective role than physical factors. The very presence of another species in the culture vessel of *T. clodiensis* affects the fitness of at least one of its loci. In other words, interspecific competition in *T. clodiensis* conditions the selective values of certain genes to a considerable degree. The analysis of this phenomenon has been recently extended to the level of intraspecific competition (Fava 1974, 1975).

With the purpose of determining in a more rigorous way the biotic factors of selection which affect the fitness of various genotypes of *T. clodiensis*, five types of experimental populations were utilized:

- 1) Populations started with equal numbers of virgin females and males of the three genotypes (pp, pP, PP) at $f(p) = f(P) = 0.5$ in Hardy-Weinberg proportions.
- 2) Populations started with equal numbers of heterozygous females and males;
- 3) Populations started with equal numbers of recessive homozygous females and dominant homozygous females, each fertilized by males of the same genotype;
- 4) Populations with virgin females and males of the three genotypes at $f(p) = 0.2$, $f(P) = 0.8$ in Hardy-Weinberg proportions;
- 5) One population as in 4) but with $f(p) = 0.7$ and $f(P) = 0.3$.

The gene frequencies in these populations were followed for about fifteen generations. The results suggest interactions between genotypes which may affect their survival. The interaction between adults and larval stages appears quite remarkable. Fitness, in *Tisbe clodiensis*, is a function of the genetic structure of the population and of population density. Certain comparisons seem to indicate that sexual selection is also involved. The selective pressure is then determined by a great number of biotic components which operate in the various stages of life cycle, similarly to what has been described by Kojima and Tobari (1969) in *Drosophila*. It seems reasonable to suggest that in *T. clodiensis*, at least under these experimental conditions, a frequency-dependent mechanism is involved. Equilibrium conditions would thus be determined

not only by heterozygote superiority but also, or prevalently, by a progressive minimization of selection coefficients as equilibria are approached.

A reasonable hypothesis to explain the mechanisms through which competing species or genotypes modify the equilibrium values of certain genes is chemical interaction. This is supported by the results of other experiments carried out to test whether, in *T. clodiensis*, the survival of a genotype from nauplius to adult may be altered by the presence of other genotypes in the same culture vessel. In a first series of experiments, the survival of nauplii, pp, was measured 1) in a monomorphic culture, 2) in the presence of adult pp females, and 3) in the presence of adult PP females. A similar experiment was carried out with PP nauplii. The results indicate survival values significantly lower for nauplii, especially PP nauplii, competing with adults of a different genotype.

The existence of such interactions between genotypes of the same species had already been detected in *Drosophila* by several authors, e.g., Lewontin, Weisbrot, Dawood, Strickberger, Huang, Singh, and Kojima (see Fava 1974, 1975 for references), who were able to demonstrate that the phenomenon is controlled by a sort of 'conditioning' of the medium by the biotic products of the various genotypes. In the case of *Tisbe*, the mechanism may be based on the production of differential toxic metabolites. In conclusion, the importance of biotic factors in *T. clodiensis* could be sufficient to justify the peculiar type of geographic isolation occurring in this species.

The hypothesis of chemical mediators may help in the interpretation of some mechanisms responsible for the difference in 'evolutionary histories' often observed in fouling communities. Allee suggested as early as 1934 that aquatic biological associations may condition the surrounding medium by means of secretions or excretions, whose nature and biological effect are one of the most significant problems of sinecology (or 'mass-physiology', to use Allee's term).

These chemicals may have trophic functions, as shown in Provasoli's (1963) brilliant research, defense functions, or oligodynamic functions. The latter operate between individuals belonging to different species, by means of 'allelochemics' (Whittaker and Feeny, 1971); or, when individuals of the same species are considered, by means of pheromons or self-inhibitors. The pheromons act on the reproductive behavior, on the social regulation and recognition, and on the territorial delimitation. The self-inhibitors act mainly by checking population densities. The theory of the ecological importance of certain organic compounds in the sea, viewed as factors involved in

competition, succession and integration of marine communities, is especially to Lucas' (1955) credit. The use of the term 'ectocrines' to indicate those external metabolites endowed with similar oligodynamic properties has also been introduced by Lucas.

As Pourriot (1966) states, consideration of physical factors, of the mineral chemical constituents, and of the trophic inter-organismic relationships, is not sufficient to explain the structure of the aquatic communities, and even less their variability in time and space. The discovery of external metabolites acting as chemical mediators may hopefully help to explain the complex phenomena of mutualism and antagonism involved in the regulation of communities.

To give an example, Aubert and coworkers (see Sarà, in press, for reference) have recently described a periodic system of antibiotics in unicellular planktonic algae such that the biosynthesis of antibacterial substances can be activated or inhibited by certain chemicals according to the season. Among the various cases illustrated by these French authors, I shall mention the one concerning the relationships between the dinoflagellate *Prorocentrum micans* and some diatoms: the former seems to produce a mediator (a protein having a molecular weight of ca. 50,000) capable of inhibiting the antibiotic synthesis in the diatoms, which, in turn, would produce a mediator (possibly, a nucleoprotein) capable of inducing in the dinoflagella the synthesis of the inhibitor. Feedback mechanisms of this sort, which appear to be widespread in the marine environment, could account for certain otherwise obscure variations in the equilibria of phyto- and zooplankton populations.

The effects of external metabolites are not confined to pelagic life, but also concern interactions among benthic organisms. For example, organisms of a species may produce substances which, although undefinable '*sensu strictu*' as pheromons, can nevertheless influence other individuals of the same species, by inducing self-antagonistic reactions leading, in the case of very high population densities, to an arrest of growth and reproduction. Knight-Jones and Moyse (1961) extended this sort of control mechanism of intraspecific competition to several benthic organisms like ascidians, bryozoans, and sponges. They cite another example, in the life of sessile organisms, where a special role is played by substances which attract larvae, thus inducing them to settle on substrates favourable to their further development. The fixation mechanisms in *Balanus balanoides* and other barnacles are quite well studied -- starting with the early investigations by Knight-Jones (1953) on gregarious behavior and continuing

up to the recent identification of the inducing substances as glyco-proteins and nucleic acids (Gabbott and Larman, 1971).

Also important for the analysis of the recognition mechanisms are Crisp's (1974) observations, according to which the substance responsible for attracting the cyprids of *B. balanoides* and *Elminius modestus*, would be the so called 'arthropodin', a heat-stable proteic component of the cuticle. It seems that the reaction to the stimulus takes place through the recognition of a special molecular configuration of the 'arthropodin'.

In phenomena of this sort (see also Scheltema, 1963), which often imply a precise specificity of action, genetic factors must necessarily be involved. Doyle (1975) recently attempted to construct a theory of 'habitat selection in varying environments', especially concerning the settlement of planktonic larvae of sessile marine invertebrates. With the objective of predicting whether larvae will exhibit habitat preferences, settlement behavior is treated as a Markov chain in which the transition probabilities are the probabilities of encountering a substrate, of metamorphosing on it, of surviving to the adult stage, or of dying in the plankton. The model is illustrated by the results of observations on the serpulid tube-worm *Spirorbis borealis*. The relative attractiveness of fucoid algae as substrates for larvae is shown to differ between populations of *Spirorbis*. Knight-Jones *et al.* (1971) believe that these interpopulation differences in *Spirorbis* might not be due to a non-genetic 'conditioning' of the larvae during embryogenesis. But even if the genetic aspects of preferential settlement have not yet been studied experimentally, a possible clue to the problem is provided by the variety of investigation tools available today to the marine ecologist. It will thus be possible to test Doyle's predictions concerning patterns of dominance and additive genetic variation in preferential settlement of larvae. A proper utilization of electrophoretic techniques might also permit us to evaluate the extent to which the structure of the fouling community depends on the genetic structure of the constituent species.

Another important aspect of the fouling community lies in its possible utilization as an indicator of environmental quality (Relini, Barbaro and Francescon, 1972). According to Redfield and Deevy (1952), this community may be regarded as a climax which is characteristic of the particular substrate and locality. In other words, its structure may reflect the changes, natural as well as artificial, to which the environment is subject in time and space. It is reasonable to assume that what applies to the community as a whole, applies also to its species

members, whose genetic make-up may be expected to reflect selective environmental changes. Some benthic sessile organisms, such as *Mytilus*, provide a most favorable material for studies aiming to establish if and to what extent a particularly deteriorated environment may affect the genetic structure of its populations. Research of this kind is now being carried out in our laboratory, and the first results appear quite promising.

Other benthic organisms, such as *Gammarus*, *Tisbe*, or *Nereis*, could also be utilized for detecting the possible development of genetically induced tolerance to certain pollutants. A few years ago, Bryan and Hammerstone (1971) studied the adaptation of the polychaete *Nereis diversicolor* to estuarine sediments containing high concentrations of copper. High copper animals survive in polluted areas because they have developed a tolerance to the toxic effects of copper which is neither readily lost nor readily acquired by non-tolerant animals. The situation is similar to that found on old mine dumps, where populations of metal tolerant land-plants have evolved. McNeilly and Bradshaw (1968) were able to demonstrate the genetic nature of this acquired tolerance to copper in *Agrostis tenuis*.

In conclusion, the investigations reviewed above are examples of the growing importance of a multidisciplinary approach for a better understanding of the factors governing the origin and evolution of fouling communities. These, at the same time, provide a new tool for tackling a variety of problems which require for their solution observations in nature combined with laboratory experimentation.

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SOME CURRENT PROBLEMS IN MARINE GENETICS

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INTRODUCTION AND BACKGROUND

There is a large and widely scattered literature on the development, morphology, physiology, and behavior of marine invertebrate larvae. Investigators have frequently noted intra- and interpopulation variability in these traits and have ascribed this variability, in part, to genetic differences. Although such oblique references to larval genetics are common, there are at present very few papers on larval genetics outside of the specialized literature of shellfish mariculture. I shall use the dearth of primary literature as license to broaden the scope of this review to general problems of marine genetics and dispersal.

The genomes of organisms have always been regarded as black boxes, and for good reason: one can study morphology if one has only the animal, physiology if one has the living animal, but genetics only if the animal will cross and reproduce in the laboratory. The few marine invertebrates with which controlled crossing has been achieved, such as Dr. Bruno Battaglia's *Tisbe*, have yielded much valuable information. Although there is no substitute for the genetic dissection of organisms by controlled crosses, linkage study, and karyotype analysis, much can be learned from allozyme studies of organisms. Allozymes are protein mobility variants on electrophoresis gels resulting from mutational alterations of the corresponding structural genes. Allozyme patterns are translatable into single-locus genotypes of individuals, and these in turn are pooled into the basic parameters of population genetics, the frequencies of genotypes and alleles in populations. Since the inception of allozyme studies over a decade ago, it has been possible to extract genotypes of up to about thirty protein loci from genome black boxes.

Larvae are prereproductive individuals by definition

and so are a step removed from the fundamental process of microevolution, the differential reproduction of phenotypes and correlated genotypes. This does not reduce their importance in adaptation and evolution. The unconscious supposition that a larva is only the unformed precursor to the adult organism, like the acorn to Aristotle's oak, will not stand examination. All stages of the life cycle are equally faced with adaptation to the immediate environment while simultaneously fulfilling functions that have adaptive meaning only to later stages. Thus, adults consume energy reserves in manufacturing gametes; and dispersing larvae experience mortality in locating substrates suitable for adult feeding, growth and reproduction. Species with planktotrophic larvae are temporally polymorphic, with the larval stages as the agents of dispersal and the adult as the reproductive stage. This functional division of the life cycle means that the unit processes of evolution act somewhat differently in larvae and in adults. The most important of these processes are recognized as (i) mutation, (ii) random drift, (iii) migration and gene flow, and (iv) natural selection.

(i). Larvae are not the progenitors of mutations except those occurring in the rudiments of germinal tissue, and they do not transmit mutations. However, the adaptability of a new mutation is first tested by the larvae, provided the mutant locus is functional at that stage.

(ii). Random drift varies inversely with population size, whereas the local population size of a species is usually at its peak shortly following reproduction. Dispersal and mortality may decrease the larval density so much that new habitats are colonized by a few individuals each. Aggregative tendencies of larvae or their attraction to specific habitats or conspecific adults oppose this attenuation. Small-scale colonization brings about drift by the *founder principle*, the random alteration of gene frequencies due to the sampling error arising in the founding of a small gene pool from one much larger. There will also be a loss of heterozygosity amounting to about the fraction $\frac{1}{2}N_e$ during the foundation episode, where N_e is the number of effectively (and randomly) breeding colonists (Crow and Kimura, 1970).

(iii). Marine larvae are functionally analogous to plant propagules. They additionally may be self-sustaining (planktotrophic larvae) and exercise some choice of settling site. In dispersing animal species it is normally the young prereproductive animals that migrate (Wilson, 1975). This is undoubtedly an evolved response, since these individuals have the highest reproductive value. The reproductive value, v_x , is the relative number of female

offspring that remain to be born to each female of age x , and is calculated from age-specific survivorship and fertility rates. The v_x in dispersing species would probably be at its highest in settling larvae which had already experienced the severest mortality, but had not yet begun reproduction.

(iv). Natural selection operates from the time of gamete formation until the v_x of survivors reaches zero. Through mortality, selection acts negatively, as a culling agent of phenotypes and genes. This is the only mode of selection in larvae, which can only be conservators of genes. Among surviving adults there will be variance in genetic adaptability which will result in variance in transmission of genes to the next generation. This more positive aspect of natural selection applies to genes but not to genotypes which are broken down into constituent genes and linkage groups in meiosis of dioecious and outcrossing monoecious organisms. On the other hand, much or all of the successful parental genotype can be passed on intact in asexual reproduction, thelytokous parthenogenesis, and self-fertilization.

On the whole, parthenogenesis and selfing are subsidiary to bisexuality in marine invertebrates (reviews of marine reproduction in Gardiner, 1971, and White, 1973). This means that the survival-tested parental genotypes are not conserved. From this fact it has been inferred that temporal variability of the parental environment makes it an uncertain predictor of reproductive success of offspring (Williams, 1975). A better strategy is to couple the variability generating feature of sexual reproduction to the dispersal capabilities of larval migration to maximize the number of habitats occupied and improve the match between some of the new genotypes and their environment. Many members of the fouling community, such as sponges, hydroids, bryozoans, and ascidians, employ a double strategy by which the original genotypes are extended spatially *in situ* by colony formation while long range colonization is by larvae resulting from sexual reproduction (Williams, 1975).

Mutation, drift, gene flow, and natural selection interact to effect evolutionary change. At the present time it is not known whether evolution is brought about principally by the cumulative changes at many independent loci, or by non-additive multi-locus epistatic effects. There is some evidence in vertebrates that changes at regulatory rather than structural loci are most significant in evolution (King and Wilson, 1975; Wilson, Maxson and Sarich, 1974). Operationally, population biologists assume that the unit process in evolution is a change in allele frequency at single loci. This level plus the investigation of

linkage or selective association of alleles at a few loci is all that can be handled in allozyme genetics studies. This is also the level of this review.

Mutation is too slow a process to figure importantly in short-term genetic studies of natural populations. Random drift, gene flow, and natural selection can be very important over single generations. The magnitude of drift is a function of population size and breeding structure, that of effective gene flow is a function of the proportion of migrants and genic differences between exchanging populations, and that of natural selection is a function of the fitness variance in the population (Fisher's fundamental theorem, 1930). The effects of genetic drift are to diminish genetic variability within populations (by $\frac{1}{2}N_e$ /generation) and to genetically differentiate non-exchanging neighboring populations. Both effects are expressed by f , the inbreeding coefficient of a population and the variability of gene frequencies among subdivided populations. A measure of the latter calculable in allozyme studies is the ratio of variance of allele frequencies among populations to the theoretical variance if all populations were fixed for one allele or another (Lewontin, 1974).

$$f = \frac{\sigma^2_p}{\bar{p}(1-\bar{p})}$$

\bar{p} is the mean value of the frequency of p over populations.

Migration and gene flow reduce the rate of subdivision by drift. At equilibrium between migration and drift (Wright, 1940):

$$f = \frac{1}{1+4N_e m}$$

where m is the proportion of genes received each generation from an infinite pool of genes. Practically, this formula is difficult to use because N_e and m are likely to be unknown. Originally Wright (1940) utilized this formula in his *island model* of migration, in which all "islands" or clusters of animals exchange genes equally with all others and the population size of each island is identical. These requirements are clearly unrealistic for marine larva. There is also a family of *continuous models* of migration and drift in which a single continuous population of constant standing density of 1-, 2-, or 3-dimensions is assumed, and *stepping-stone models*, which envision equal-sized population clusters strung out linearly or at nodes of a rectangular lattice exchanging migrants isotropically in one or more dimensions with adjacent populations only.

Variant models also include a long distance migration parameter. Kimura and Weiss (1964) give the following formula for gene frequency variance over populations in a 1-dimensional stepping-stone model, with m as short-distance migration and m_∞ as a lower rate of long-distance migration:

$$\sigma_p^2 = \frac{p(1-p)}{1+4N_e \sqrt{2m m_\infty}}$$

Natural populations will not, of course, be of equal size nor will migration be isotropic. Dimensionality will also not be a whole integer. The latter can be estimated by counting the number of populations within each concentric radius r from an initial population (Cavalli-Sforza and Bodmer, 1971). The number of populations will be independent of r in a 1-dimensional distribution, but will be an exponential function of r in multi-dimensional arrays. The number of dimensions will be the exponent of r plus 1. In the Parma Valley of northern Italy, the 2-dimensional model gives the best fit to village distributions of humans, but dimensionality is intermediate between 1 and 2 at high altitudes (Cavalli-Sforza and Bodmer, 1971). In the sea, dimensionality is doubtless greater on the continental shelf than in narrow estuaries like Chesapeake Bay. In stepping-stone models genetic correlation falls off with distance least rapidly in the 3-dimensional distribution and most rapidly in the 1-dimensional distribution.

The migration formulas make too many simplifying assumptions to be helpful to marine biologists, except in a general way. They do have potential utility. Of the parameters p , \bar{p} , N_e , and m , p and \bar{p} can be routinely determined for several loci by allozyme electrophoresis. It should be possible to approximate N_e in some cases, leaving m , the proportion of migrants, determinable from the amount of genetic differentiation among populations. However, the assumption must be made that natural selection has no effect on gene frequencies, and this assumption is presently unwarranted.

If allozyme alleles are alike in adaptive value they are selectively neutral. Their utility in population studies would then be as neutral markers for the action of drift and migration. If they are unlike in adaptive value they will be selectively discriminated by the environment and they lose much of their value as markers. For example, an allele that has a uniformly high adaptive value over several populations will resist drift, and the variance of gene frequency over the populations will be smaller than the N_e would predict. On the other hand, if

the adaptive value of the allele is highly variable among populations, rapid genic differentiation will result, mimicing the effects of rapid drift and low migration rate. Since drift and migration inevitably affect all loci of the genome at which gene frequencies differ, while selection may act differently locus-by-locus, it is occasionally feasible to determine if selection is operating or not. Nevertheless, the usefulness of polymorphic allozyme loci would be greatly clarified if it was known whether most alleles were neutral or selected. There is a burgeoning literature on neutralist versus selectionist interpretations of allozyme polymorphisms, and it would be inappropriate to pursue this subject here. Most field and experimental evolutionists are selectionists by inclination and they have assembled considerable evidence for genetic patterns in nature that support their view.

MEASURES OF GENETIC DISTANCE AND SIMILARITY

When two populations are compared at an allozyme locus, they may show any amount of genetic difference. Statistically non-significant differences in allele frequencies indicate, of course, no detectable differentiation. Higher levels of differentiation are indicated by: (1) identical alleles present, but at significantly different frequencies; (2) partially non-overlapping suites of alleles present; and (3) no alleles in common. Several coefficients or indices of genetic distance have been formulated to express differentiation usually on a numerical scale from one to zero. Of the commonly used coefficients two, those of Rogers (1972) and Nei (1972), utilized allele frequencies and one, that of Hedrick (1971), is based on genotype frequencies. Allele frequencies are more appropriate for estimating evolutionary distance (as predicated on shifts in frequency and substitution of alleles) within and between taxa. Genotype frequencies better reflect actual gene distributions over an area, and additionally take into account the breeding structures of the populations. For example, all indices work well for loci in Hardy-Weinberg equilibrium for which their mutual correlation coefficients are high (about 0.97; Hedrick, 1975), but only the Hedrick index is sensitive to departures from the H-W equilibrium, indicating possible inbreeding or migration. The Hedrick index, by way of example, is given below:

$$I_{x \cdot y} = \frac{\sum_{j=1}^n p_{j \cdot x} p_{j \cdot y}}{\frac{1}{2} (\sum_{j=1}^n p_{j \cdot x}^2 + \sum_{j=1}^n p_{j \cdot y}^2)}$$

$P_{j,x}$ is the frequency of the j th genotype in population x , and the number of genotypes is n .

Indices of genetic similarity are usually presented in a $N \times N$ matrix. Generally the indices of all polymorphic loci, or even monomorphic loci, are pooled to give the best estimates of genetic distance. As Hedrick (1975) points out, this procedure loses much information because patterns of different loci are often discordant over the same geographic range.

THE RELATION OF ALLOZYME AND PHENETIC DIFFERENTIATION

Surveys of 15-30 protein loci have been completed in dozens of vertebrate and invertebrate species in order to obtain estimates of genetic variability. At the present time the most comprehensively examined groups are man and the other primates, small rodents, some salamanders and lizards, and species of *Drosophila*. Among marine invertebrates, *Mytilus* (Boyer, 1974; Koehn and Mitton, 1972; Levinton, 1973 and several studies pending; Milkman and Beaty, 1970; Mitton, Koehn, and Prout, 1973), and to a lesser extent *Littorina* (Berger, 1973; Gaines, Caldwell and Vivas, 1974; Snyder and Gooch, 1973), the ectoproct *Schizoporella* (Gooch and Schopf, 1970; Gooch and Schopf, 1971; Schopf, 1973) and the polychaete *Capitella* (Grassle and Grassle, 1974) are best characterized.

The proportion of polymorphic allozyme loci in invertebrate populations ranges between 25 to 75 percent (Avise, 1974). *Drosophila* studies weight these estimates heavily, but they are probably substantially correct for marine invertebrates. Range-restricted small populations cut off from gene flow and probably inbred show lower levels of genetic variability (Avise and Selander, 1971; Webster, Selander and Yang, 1972). Other generalizations for invertebrate genetic patterns are that monomorphic populations are usually fixed for the same allele throughout the species range, and that variance in allele frequencies over populations tends to be lower in invertebrates than in vertebrates (Avise, 1974). Acceptance of these conclusions should be tempered by the realization that most geneticists regard *Drosophila* as the "typical" invertebrate and extrapolate accordingly.

Avise (1974) also tabulates average values of Rogers' coefficient of genetic similarity of conspecific and congeneric populations for 11 genera of vertebrates and 1 of invertebrates (*Drosophila*). Coefficients range between .75 and .98 for conspecific populations and .21 and .84 for congeneric populations. Clearly there is general

parallelism between allozyme genetic distance and degree of separation based on phenetic or breeding criteria. Nevertheless, there is no one value that indicates the threshold of speciation, and the conspecific and congeneric indices do overlap somewhat.

If indices of genetic distance regularly correlated with phenetic differentiation allozyme methods could be used with confidence in studies of evolution and taxonomy. In the *Drosophila willistoni* complex of species, allozyme differences have served to distinguish sibling species (Ayala and Powell, 1972; Ayala and Tracy, 1973). The ectoprocts *Bugula stononifera*, *B. simplex*, and *B. turrita* from Cape Cod, Massachusetts (Gooch and Schopf, 1970, and unpublished) show moderate phenetic differences, but their protein patterns of esterase, and malate dehydrogenase gels are quite unlike (Fig. 1). In these examples genetic differentiation at the protein loci exceeds phenetic differentiation.

Protein patterns for the species pair of wharf crabs *Sesarma cinereum* and *S. reticulatum* at 10 loci generally show small mobility differences, indicating that at the majority of loci the two species are fixed or segregating for different alleles at homologous loci (Fig. 1). A few alleles are shared by the species (Gooch, submitted for publication). Here, small phenetic differences are paralleled by approximately equivalent genetic differences.

Several recent studies have shown that phenetic differentiation can also greatly outstrip genetic differentiation. M. S. Johnson (1975) investigated allozyme variation in 3 species of fish of the genus *Menidia* (Teleostei, atherinidae), *Menidia menidia*, *M. beryllina* and *M. peninsulae* along an extensive Atlantic Coast transect of North America. At least 2 of the 3 species are sympatric over much of the range between New England and Texas, and the author tested for concordant variation to salinity and temperature gradients. To summarize a good deal of complex data, alleles at some loci in some species comparisons varied concordantly but most did not. More to the immediate point, *M. menidia* is quite variable phenetically over the transect, but there is much less genetic variation. *M. beryllina*, on the other hand, is more variable in allozyme frequencies than phenetically. Protein genetic differences cannot be used as a reliable predictor of phenetic differences in the genus.

More striking is the study of B. J. Turner (1974) on 5 species of the genus *Cyprinodon* (pupfish) inhabiting mostly disjunct streams and lakes of widely varying temperature and salinity of eastern California desert basins. The species of pupfish are all readily distinguishable in meristic and quantitative traits, dentition and behavior.

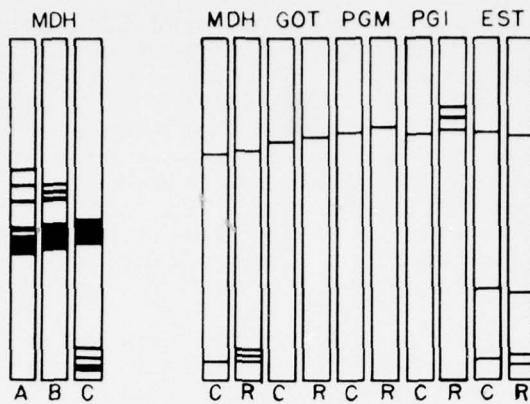


Fig. 1. Typical enzyme mobility patterns for congeneric species. Malate dehydrogenase (MDH) patterns are composed of similar elements with strikingly different mobilities in the Bryozoans *Bugula stolonifera* (A), *B. turrita* (B), and *B. simplex* (C). The brachyuran crabs *Sesarma cinereum* (C) and *S. reticulatum* (R) differ only slightly in mobility at malate dehydrogenase (MDH), glutamate oxaloacetate transaminase (GOT), phosphoglucomutase (PGM), phosphoglucose isomerase (PGI), and esterase (EST) loci.

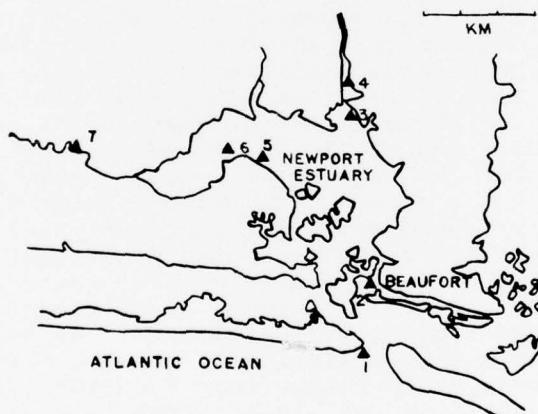


Fig. 2. The *Balanus* transect from Fort Macon to the Newport River near Beaufort, North Carolina. Localities are given in Table 2.

Protein phenotypes for 31-38 inferred loci were determined in all species and many proved to be identical. The indices of genetic similarity in the species matrix ranged between .808 and .968; indices were simply a proportionality of allele-divergent to allele-same comparisons, which should yield values fairly similar to those of the Rogers' index, (Yang, Wheeler and Bock, 1972). These interspecific coefficients are in the middle of the intra-species range as given by Avise (1974), and again show that range disjunction, phenetic differentiation, and speciation can occur without much differentiation at protein loci.

A last example is that of the land snail of the genus *Cerion* investigated near the settlement of Pongo Carpet on Great Abaco in the Bahamas (Gould, Woodruff and Martin, 1974). *Cerion* is famous for its extreme phenetic diversity on islands of the West Indies. It seemingly has undergone, as Gould, *et al.* put it, "protean speciation", with over 300 species reported from the Bahama Islands alone (Clench, 1957). An undescribed population isolate of snails near Pongo Carpet was phenetically quite different from *C. bendalli* over a kilometer distant. It initially seemed deserving of specific status. When subjected to complex multivariate analysis of 19 morphological attributes of the shell and to an electrophoretic comparison of 18 protein loci, no sharp differentiation was found. The morphometric study revealed an essentially clinal gradient of characters, and the genetic data gave evidence of virtually no differentiation (Nei index of similarity of 0.98-0.99). The authors concluded that the Pongo Carpet population, in spite of its phenetic distinctiveness, is only a geographic variant of *C. bendalli*. Their study also throws doubt on the legitimacy of the hundreds of described species in this genus. Here the situation is exactly opposite of that in *Drosophila willistoni*; morphologically sibling species may possess marked underlying genetic differences, while conversely there may exist enormous phenetic diversity in some species without accompanying genetic differentiation. That phenetic and structural genic evolution and even speciation are not always closely coupled is an important recent finding of geneticists. It seems increasingly likely that evolutionary changes are mediated primarily by regulatory rather than structural loci (Wilson, Maxson and Sarich, 1974). The implication for marine genetics is that the Mendelizing and biochemically-detected genes, which are the experimental basis of the entire evolutionary literature, this review included, may be of only secondary importance in adaptation and evolution.

GENETICS OF INVERTEBRATE LARVAE

The extension of protein genetics to larvae would be of considerable interest. It would then be possible to utilize particular alleles as tags or markers of populations, and to follow cohorts of maturing individuals for systematic shifts in allele frequency that would indicate the operation of natural selection. As was stated earlier, allozyme alleles should best serve as population markers if they were adaptively neutral; differences between populations would then give information about the amount of migration. If adaptive values of genotypes vary geographically natural selection might give rise to discontinuities or clines between populations that would otherwise be ascribed to low gene flow.

One study of the American eel, *Anguilla rostrata*, does suggest that selection can appreciably alter allele frequencies within a single generation (Williams, Koehn, and Mitton, 1973). This species breeds over a small oceanic area and the leptocephalus larvae are current-dispersed to the American coast from northern South America to the Arctic. Larvae subsequently metamorphose into elvers which then enter estuaries and coastal streams. Adults return to pool their gametes in the same circumscribed area, and it is thought that larvae are unable to navigate to specific coastal localities. Five polymorphic loci were investigated, mainly in young elvers, in populations from Newfoundland to Florida. Four loci showed significant geographic differences in allele frequency, 3 clinal latitudinally, and one varying unsystematically. The most common allele at a phosphohexose isomerase locus (PHI), for example, varied in frequency by about 0.15 over the transect. An investigator knowing nothing of the life cycle of *Anguilla* might suppose that the PHI cline was an artifact of isolation by distance or perhaps was established selectively over a long period in response to the latitudinal shift of environment. If the life-cycle of the eel is correctly understood, however, genetic differentiation must be due to selection over each single generation. Selection may operate primarily on larval genotypes during the long migration to the coast rather than *in situ* among elvers and adults; evidence on this point is lacking.

The blue mussel, *Mytilus edulis*, has proved to be a good research subject. Relevant papers were cited in an earlier section. Dr. Jeffrey Levinton is the reigning mytilid expert and he will report his findings concerning eco-genetic strategies of bivalve species under different levels of environmental heterogeneity at this workshop. I shall briefly review the recent work of J. F. Boyer (1974)

on size-dependent variation at the LAP (Leucine aminopeptidase) locus in populations of *M. edulis* on Cape Cod. This species segregates for three LAP alleles, S, M, and F (slow, middle and fast mobilities on gels) throughout its range from Nova Scotia to North Carolina. Allele frequencies are known to vary appreciably from Long Island to north of Cape Cod. Boyer sampled large populations of mussels of different size classes from the mouths and intermediate and upstream sites of 2 tidal streams and obtained allele frequencies at the LAP locus. Here there are no direct data of larval allele frequencies; but frequencies can be followed in small (presumably young where environmental severity can be discounted) to large (old) adults in the same locality. Allele frequencies of recently-settled individuals should reflect parental allele frequencies after subsequent modification by selection in the larvae, and those of old individuals should record the selective adjustment to the local site. Since larval dispersal is considerable, most settlers will not have been recruited locally and may not be well matched genetically to local conditions, thus accentuating the chances of finding (1) size-specific shifts in allele frequencies, and (2) deviations from the H-W equilibrium as particular genotypes drop out. The frequency of S proves to be homogeneous over all populations in mussels smaller than 15 mm. There is increasing heterogeneity of larger size, however, with both streams showing a clinal decrease in S upstream in larger individuals. Both stream mouth populations show increase in S and both upstream populations decrease in S with increasing mussel size. Natural selection is clearly operating although it is impossible to determine whether a specific locus is selected or an entire linked group of genes in a one-locus study. All population samples and size distributions show significant deficiencies of heterozygotes (SM, SF, MF). This may indicate inbreeding or it may be due to mixing of genetically distinct larval populations.

A direct study of larval genetics was made on the xanthid crab *Rhithropanopeus harrisii* (Gooch, recently submitted for publication). This small estuarine crab sheds its larvae into the water which then undergo 4 zoeal and a megalops stage before metamorphosing into adults. Its geographic range is enormous, extending from New Brunswick south to the Gulf of Mexico and possibly to Brazil, with populations also reported from California and the Baltic Sea (literature summarized by Costlow, Bookhout and Monroe, 1966). Zoea, megalops, and adult stages were obtained from 3 stations between Maine and North Carolina and were electrophoresed and stained for 16 protein systems. Third and fourth instar zoea and

megalops were run individually according to standard procedures, but in miniature: starch ribbons 2 mm thick and 10 cm long were utilized, and samples were applied to 1 mm square pieces of Whatman #1 filter paper.

The investigation was undertaken to help clarify three problems: (1) the technical feasibility of allozyme studies of invertebrate larvae; (2) the differences, if any, in protein patterns of larval and adult stages; and (3) the possible differences in allele frequencies among latitudinally separated populations. In answer to (1) above, 6 stain systems yielded well-resolved bands in zoeae, 7 systems in megalopa, and 10 in adults. Based on this experience I believe that organisms down to about 0.5 mm in diameter can be used successfully in allozyme studies with only slight modification of usual methodology. No doubt the threshold can be lowered if special micro-methods are employed. Enzyme systems that commonly stain well in small tissue samples of animals of a variety of phyla are phosphohexose isomerase, NAD-dependent malate dehydrogenase, esterases, phosphoglucomutase, leucine-aminopeptidase, and (snake-venom requiring) peptidase.

Band patterns were also identical in larval and adult *R. harrisii*, except that some low-assay systems in adults could not be discerned in larvae. This result is somewhat surprising, since the genes functional in adults might be different from those in larvae. If this identity is generally true of invertebrates, it holds promise that larvae taken in plankton hauls might be identifiable to species by their band patterns.

Except for a polymorphism at the peptidase locus in the intermediate Chesapeake Bay population, all of the loci proved to be monomorphic for the same allele throughout the transect. Therefore, almost no genetic differentiation was discovered, and any index of genetic similarity based on the 10 loci would be near 1.00. It would be interesting to discover if monomorphism and genetic uniformity prevails over the larger range of *R. harrisii*, but this has not been attempted.

GENETIC-GEOGRAPHIC PATTERNS IN MARINE SPECIES

The plotting of allele frequencies of population samples over a transect, as for coastal or estuarine species, or on a 3-dimensional map, as for terrestrial or oceanic species, will usually reveal a geographic pattern. Allele frequencies may be relatively homogeneous regionally, show more or less consistent clinal trends, or reveal sharp discontinuities. Either natural selection or

some combination of drift and migration can be made to account for any pattern (Lewontin, 1973). A cline, for example, can represent genetic adjustment to a gradient of shifting adaptive values or it can be a diffusion path between genetically contrasting populations. Geographic patterns cannot be more than *prima facie* evidence for selection unless the correlation between allele frequency and identifiable environmental parameter is extraordinarily close, or unless selection can be shown to be operative in a laboratory analog of the natural environment.

Drift and inbreeding promote population subdivision, and migration and gene flow retard subdivision. This will be true whatever the effects of natural selection, and so freely-exchanging populations will normally be more genetically homogeneous than those with weak powers of dispersal. Allozyme work to date suggests that good dispersers such as invertebrate species with planktotrophic larvae, are less genetically differentiated over large distances than those lacking effective means of dispersal (review in Gooch, 1974). Dr. Scheltema's work on trans-oceanic migration in molluscan larvae (1971) has this import also.

An example of a species that appears to be genetically homogeneous over a long coastal transect is the mud snail, *Nassarius obsoletus*. Adults of this species occur abundantly on intertidal flats of the Atlantic Coast of North America. There is a planktonic larva stage of perhaps two weeks or longer, depending on water temperature and suitability of substrate (Scheltema, 1961; 1965). Snails collected in 1969 and 1970 proved to be very similar in allele frequencies at a malate dehydrogenase and a non-specific protein locus in a transect of about 1000 km from Cape Cod, Massachusetts to Beaufort, North Carolina (Gooch, Blake and Knupp, 1972). The Hedrick index of genetic similarity was between .87 and .99 in all comparisons (Snyder and Gooch, 1973). The terminal points and one intermediate locality were recollected in 1972 and two new polymorphic loci, isocitrate dehydrogenase and peptidase, were scored. The allele frequencies of the 4 loci are given in Table 1 (Snyder and Gooch, 1973, and unpublished data). Borderline significant variation exists in some inter-population comparisons, but, on the whole, allele frequencies are only weakly differentiated.

Genetic homogeneity at polymorphic loci may be maintained by uniformly acting selection involving some kind of net heterozygote superiority (so that one allele does not go to fixation) or by migration. The selection hypothesis becomes less tenable as the environments of the populations become more highly differentiated. In the case of *N. obsoletus*, snails throughout the transect

Table 1.

Allele frequencies at isocitrate dehydrogenase (IDH), lactate dehydrogenase (LDH), peptidase (PEP), and nonspecific protein (PT) loci in *Nassarius obsoletus*. The localities are Woods Hole, Massachusetts, Assateague, Maryland, and Beaufort, North Carolina. Alleles are symbolized by letters in order of increasing anodal mobility of their products.

Locus, allele, and sample size		Woods Hole	Assateague	Beaufort
<u>IDH</u>	N	(50)	(42)	(80)
<u>a</u>		.760	.762	.894
<u>b</u>		.240	.238	.106
<u>LDH</u>		(50)	(47)	(77)
<u>a</u>		.550	.574	.519
<u>b</u>		.450	.426	.461
<u>c+d</u>		.000	.000	.020
<u>PEP</u>		(49)	(44)	(80)
<u>a</u>		.041	.057	.119
<u>b</u>		.245	.148	.237
<u>c</u>		.398	.557	.388
<u>d</u>		.245	.091	.206
<u>e+f</u>		.071	.147	.050
<u>PT</u>		(33)	(47)	(76)
<u>a</u>		.697	.660	.730
<u>b</u>		.303	.340	.263
<u>c</u>		.000	.000	.007

encounter a similar environmental range, though with lower temperatures at all seasons in the north. It is probable that the alleles at the four sampled loci are insufficiently discriminated by selection to overcome the homogenizing effects of migration.

During the summer of 1973 my student, Mr. Douglas Baker, conducted a survey of allele frequencies at two loci in each of the cirripede species, *Balanus amphitrite amphitrite*, *Balanus eburneus*, and *Balanus improvisus* from the Beaufort Inlet to the head of the Newport River estuary in North Carolina. This transect is only about 18 km long, but the environment varies from nearly normal marine at Beaufort Inlet, with relatively constant salinity and seasonal variability in temperature, to widely fluctuating estuarine conditions at the head of the Newport River. In 1956, for example, salinity varied from 0.6 to 33.4‰ at Cross Rock, which is station 5 of Figure 2, and the temperature varied from below 5° C to above 30° C there (Wells, 1961). This range of conditions is comparable to that encountered by *Nassarius obsoletus* over its much longer transect. In amplitude of short-term fluctuation, it greatly exceeds that of the snail.

The three species *B. amphitrite amphitrite*, *B. eburneus* and *B. improvisus* are adapted to increasingly estuarine conditions in the order above, and they have overlapping distributions in the Newport River estuary. *B. amphitrite amphitrite* is dominant at the Beaufort Inlet, and only *B. improvisus* exists in the Newport River proper (station 7). Phosphohexose isomerase and malate dehydrogenase polymorphic loci were surveyed in the three species in an effort to find systematic changes in allele frequencies or differences in amount of genic variability along the transect. Table 2 summarizes the data. First, inspection shows little if any genetic differentiation for any species over the stations. Second, the alleles, a - d, which are probably homologous based on the rank order and comparative mobilities of their enzyme products, have very similar frequencies in all three species. *B. amphitrite amphitrite* a, b, and c MDH alleles at Beaufort Inlet are in the proportion 0:1.00:0. In *B. eburneus* in the Newport River at less than 1‰ salinity, alleles a, b, and c are proportionally 0:0.80:0.20. In other words, genetic homogeneity obtains not only within species but also to some degree (Table 2) between species over an environmentally differentiated transect.

The nauplius larvae of barnacles are very abundant throughout the Newport River estuary (Austin Williams, pers. comm.). It is probable that migration is extensive and that local populations are recruited from larvae of highly mixed provenance. If each species is regarded

Table 2.

Allele frequencies along the Beaufort Inlet - Newport River transect in 3 species of *Balanus*. Loci are phosphohexose isomerase (PHI) and malate dehydrogenase (MDH). Data not available for *B. improvisus* PHI. Localities are (1) Beaufort Inlet at Fort Macon, (2) Pivers Island, (3) Core Creek, (4) Intracoastal Waterway, (5) Cross Rock, (6) Preacher Point, (7) Newport River, proper.

Species, locus		LOCALITY							
allele and	sample size (N)	1	2	3	4	5	6	7	Neuse R.
<i>B. amphitrite</i>									
<i>amphitrite</i>									
PHI	N	(60)	(63)	(50)	(52)	(32)			
<u>a</u> + <u>b</u>		.025	.079	.130	.038	.047			
<u>c</u>		.900	.873	.830	.875	.922			
<u>d</u>		.075	.048	.040	.087	.031			
MDH		(46)	(63)	(50)	(52)	(31)			
<u>a</u>		0	.016	.020	.029	0			
<u>b</u>		1.000	.984	.980	.971	1.000			
<u>c</u>		0	0	0	0	0			
<i>B. eburneus</i>									
PHI		(78)	(52)	(51)	(54)	(61)			
<u>a</u> + <u>b</u>		.019	.020	.019	.065	.074			
<u>c</u>		.930	.913	.912	.889	.910			
<u>d</u>		.051	.067	.069	.046	.016			
MDH		(81)	(50)	(52)	(61)	(58)			
<u>a</u>		.080	.160	.096	.123	.164			
<u>b</u>		.908	.840	.904	.860	.836			
<u>c</u>		.012	0	0	.017	0			
<i>B. improvisus</i>									
MDH				(58)		(39)	(34)		
<u>a</u>				.026		0	.029		
<u>b</u>				.974		.796	.824		
<u>c</u>				0		.204	.147		

individually, the reasonable interpretation of these findings is that migration is of sufficient magnitude to overwhelm the differentiating action of natural selection. Thus, the estuary might be conceived as a small universe conforming to Wright's island model with a particularly high value of m . This may be the case, and if so, the results for *Balanus* are more convincing evidence for the prevention of genetic differentiation by migration in the face of an environmental gradient than that for *Nassarius obsoletus*.

However, if the similarity of frequencies of mobility-order alleles in the three species is not just a remarkable coincidence, it indicates that natural selection must be operative. The only mechanism that can maintain genetic uniformity across species is selection in which homologous alleles have similar adaptive values regardless of the species. Koehn and Mitton (1972) found evidence of similar parallelism in frequencies of inferred homologous LAP alleles in *Mytilus edulis* and *Modiolus demissus* on Long Island. The consequence of this interpretation for the barnacles is that the alleles are maintained by natural selection, but the differences in turbidity, pH, temperature and salinity do not affect their adaptive values. This inference is based solely on the genetic-geographic pattern, and is thus more suggestive than conclusive. It does point out the kind of interesting problems that genetic studies of marine invertebrates are bringing to light.

The areal genetic homogeneity of *Nassarius* and *Balanus* does not appear to be typical of marine invertebrates. Most studies have revealed geographic differentiation of allele frequencies (e.g., the citations previously made on *Mytilus*, *Littorina*, *Schizoporella* and *Capitella*). The literature to date, however, suggests that genetic divergence is rarely very great in marine invertebrates. Typical is the investigation of the mangrove periwinkle, *Littorina angulifera*, from mangrove islands off southern Florida (Gaines, 1974). Allele frequencies at an esterase locus from 20 island populations of snails were statistically non-homogeneous (range of most common allele 0.66-0.87). The populations could best be described as modestly subdivided genetically, without evidence of increasing subdivision with distance except along a gradual latitudinal cline. As usual, the geographic pattern itself provides little clue to the importance of selection, drift, or migration in its establishment. Also as usual, the amount of genetic heterogeneity over distance is rather small. The literature to date provides very few examples of strong genetic-geographic differentiation, reflecting probably the

comparative homogeneity and high dimensionality of the sea.

SUMMARY

The major points of this paper can be summarized in a few statements:

1. Population genetics provides a theoretical framework for marine genetics. Its mathematical models of population subdivision and migration apply in a general way to marine situations.
2. The fundamental parameters of population genetics, allele and genotype frequencies, are obtained rather easily in allozyme-electrophoresis studies. Allozymes can be scored in organisms at least as small as crustacean larvae. The ecological genetics of a few invertebrate genera, particularly *Mytilus*, is being actively pursued.
3. A convenient means of quantifying genetic differences is by means of indices of genetic distance. Evidence to date shows that indices are usually lower congenerically than conspecifically. This rule is not trustworthy in specific instances, and there is no simple relationship between genetic distance and phenetic differentiation.
4. Any genetic-geographic pattern can be produced by some model of interaction between natural selection, genetic drift and migration. Some studies of marine invertebrates provide strong circumstantial evidence for natural selection. Most species of marine invertebrates appear to be weakly differentiated genetically over wide areas.

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MIGRATION, SELECTION AND GENETIC DIFFERENTIATION IN MUSSELS

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The relationship of migration and selection to the genetics of marine invertebrate populations is a fundamental problem in the understanding of the adaptive significance of modes of dispersal and the evolutionary potential of genetic variability within species. I have studied the mussel *Mytilus californianus*, and determined magnitudes of geographic differentiation at several geographic scales. I have also determined the nature of microgeographic variation within the tidal zone and the dynamics of selective mortality within this zone. Two enzyme encoding loci have been identified and employed in this study with the aid of horizontal starch gel electrophoresis (leucine aminopeptidase, E.C. 3.4.1.1 and Glucose phosphate isomerase, E.C. 5.3.1.9).

Four sets of samples were taken over four scales of geography: Santa Barbara, California, to Torch Bay, Alaska (10^4 km); Cape Flattery, Washington, to San Juan Island, Washington (10^2 km); within Tatoosh Island, Washington (1 km - over the entire tide zone); and at a single locality (10^{-2} km - the same tidal height). Differences between samples are as great within Tatoosh Island samples as from Santa Barbara to Alaska. This suggests that the uniform environment of the western coastal waters of North America exerts little selective thermal gradient and that isolation by distance is probably not important in the magnitudes of genetic differentiation observed. Over the same latitudinal range, the blue mussel, *Mytilus edulis*, shows much greater geographic differentiation of the east coast of North America, reflecting the stronger thermal gradient.

The nature of the selective processes at work is indicated by many correlations of allele frequencies and genotypic frequencies with eighth above mean low water. These differences are in turn correlated with size of individuals within the population (smaller adults are found in the upper intertidal zone). At the Leucine

aminopeptidase locus studied, different genotypes were found to have differing size-frequency distributions; providing a direct means by which size-specific selection could exert changes in gene frequencies in populations through physiological shock and size-selective predation. Studies of spatfalls in successive years show that gene frequencies do not change and are selectively adapted to local environments, and that selective mortality occurs at enzyme loci between the recently settled juveniles and adults.

These studies suggest that selection maintains enzyme polymorphisms but does not identify the mechanisms by which given enzyme genotypes contribute to fitness. Current research in my laboratory involves the integration of physiological parameters with genetic variation through the use of classical dosage-mortality experiments; transplants in the field, and associated studies are now being conducted to relate these experiments to kinetic characteristics of given enzyme phenotypes and specific enzyme activity levels as a function of stress conditions.

REPRODUCTION OF MARINE BIVALVE MOLLUSCS:
A REVIEW OF SOVIET WORKS

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There is no need to discuss the importance of *Bivalvia* in benthic and fouling communities. As in other animals, the process of reproduction of these species plays a decisive role in the formation of community structure, and in the distribution and dynamics of population size. Investigations performed on molluscs are important not only for hydrobiological problems - these studies contain many facts extraordinarily useful for the understanding of some general aspects of gametogenesis, fertilization, embryogenesis and postembryogenesis.

The first Russian studies on the development and reproduction of marine *Bivalvia* appeared in the period between the end of the nineteenth and the beginning of the twentieth centuries. The prominent Russian embryologist, Zalensky (1874, 1876), described oyster development with special reference to the gastrulation and formation of germ layers. He marked the early isolation of the presumptive mantle in *Bivalvia*. The shell structure and hinge system in larvae of 20 *Bivalvia* forms from the Black Sea are given in Boris'yak's paper (1905). During the last 40 years no fewer than 100 papers concerning the reproduction and development of marine *Bivalvia* were published. Nearly 40 papers deal with the phenology and distribution of larvae and the influence of environmental factors. Gametogenesis and spawning seasons are the subjects of more than 20 papers. More than 15 publications elucidate the problems of settlement and metamorphosis. Comparatively few (fewer than 10) works on the early embryogenesis and neurosecretory regulation of reproduction have been published. In addition to the papers dealing chiefly with the reproductive aspects of *Bivalvia*, some theoretical works and reviews also consider these problems. It is necessary to note the well-known works of Mileikovsky (1959-1974) and some papers by other authors

which give special attention to the role of environmental temperature for successful reproduction and recruitment of molluscs (Zhirmunsky, 1971; Golikov, Scarlato, 1973; Andronikov, 1975; etc.).

In a large series of Mileikovsky's papers, which are predominantly reviews written both in Russian and English, different problems of the reproductive ecology of marine bottom invertebrates, including Bivalvia, are considered. In some works, Mileikovsky (1972, 1974) notes the role of larval plankton not only in the recruitment of some species of benthic animals but also in the general patterns of distribution and settling of oceanic benthos. He reevaluates the types of larval development in marine invertebrates and their distribution in the ocean according to G. Thorson; he adds the demersal type of development to the general scheme of developmental types (1971). In other works, Mileikovsky writes about the main role of temperature in determining the spawning seasons of marine invertebrates (1960, 1970c), the seasonal and daily dynamics of population size in pelagic larvae which reflect some peculiarities of their spawning (1970b), the distribution of larvae over large distances by oceanic currents (1966), the influence of pollution on larvae (1970a), and other problems of larval life. In the last paper cited above, the author claims larvae are greatly damaged by pollution during their settlement on substratum. Zhirmunsky (1971) gives attention to the different mechanisms of influence of high, low and optimal temperatures on invertebrates and writes about changes in the environmental optimum during development. Golikov and Scarlato (1973) showed that the borders of temperature optimum for successful reproduction coincided with the summer water temperature on the northern border of the species area and with the winter temperature on the southern border.

Andronikov (1975) writes that the heat resistance of gametes is constant within a species. Environmental temperature is one of the factors limiting species distribution when it is higher than the upper limit or lower than the lower limit of temperature resistance of the gametes of marine invertebrates.

In special works on molluscs, more attention was given to commercial molluscs (oysters, mussels and scallops) and shipworms. More than 20 papers are devoted to mussels; half of them are devoted to oysters, scallops and *Teredo*. At the present time, the investigations are performed on the fauna of the Barents Sea, the White Sea, and the southern and far eastern seas of the USSR. More than half of all the studies were conducted on species from the Black Sea and the Sea of Japan.

REPRODUCTIVE CYCLES

Dzyuba (1971a,b,c, 1974; Gruzova, Dzyuba, 1973) describes the reproductive cycles in female gonads of the scallop, *Pecten yessoensis*, and the mussel, *Crenomytilus grayanus*; she gives a thorough cytological description of gonadal changes during the year, and adds cytochemical and morphometrical evidence to these data. The author distinguishes 7 types of accessory cells which take part in the resorption of unspawned oocytes and possibly in the nutrition of growing oocytes. Nutrition of the oocytes was considered in connection with problems of solitary and alimentary types of nutrition. General attention may be attracted by the data on the considerable resorption of oocytes after spawning and during the winter. It is shown that the scallop spawns once a year, in the first half of the summer, and the mussel spawns twice a year, at the beginning and at the end of the summer.

Chukhchin (1965) writes on the maturation age, reproductive cycle and spawning seasons in *Chamelea gallina* from the Black Sea. He notes the absence of a resting period in gonads after spawning. The reproductive cycle in the scallop, *Swiftopecten swifti*, is described in detail by Kukin (1976). The author marks a similarity of cell types in the gonads of *S. swifti* and *Pecten yessoensis*. He gives some data on the spawning seasons in these species from Peter the Great Bay and describes the rare example of hermaphrodite gonad in *S. swifti*. Kutishchev and Drozdov (1974) give data on the sex ratio in the population of the mussel, *Crenomytilus grayanus*, and describe examples of hermaphroditism, which is probably a temporary transitional state from the male gonad to the female one.

Kasyanov, et al. (1974, 1976) determined the spawning seasons and gonadal states during the spawning seasons in common Bivalvia from Peter the Great Bay. Authors think that comparatively synchronous spawning in most of the species is connected with the high values of surface water temperature and the abundance of food for the larvae, small phytoplanktonic forms.

Karpevitch (1964) calls attention to the various patterns of reproduction in eury- and stenobiotic molluscs. A prolonged period of reproduction is common for the eurybiotic species, but is shortened - 2 or 3 months - for the stenobiotic ones. By analyzing the development and reproduction of Teredinidae in the Caspian, Azov and Aral Seas, the author shows some adaptations in structure and size of eggs and sperms to the environment. Zhuravleva and Prazdnikov (1975) discuss the acceleration of gametogenesis in the mussel, *Mytilus edulis*, with a change in salinities from 10% to 33%. A decrease in salinity to 15% accelerates the

spawning time and enforces processes of phagocytosis in the gonads.

NEUROSECRETORY REGULATION OF REPRODUCTION

An analysis of neurosecretory elements and neurosecretory regulation in the scallop and the mussel is undertaken in the papers by Varaksin (1974a,b) and Marchenko (1974, 1976a). Varaksin showed the significant extrusion of a neurosecretory material from neurosecretory cells of the scallop, *Pecten yessoensis*, which occurred just before spawning and was followed by an abrupt decrease in the neurosecretory contents of the cells. In the mussel, *Crenomytilus grayanus*, the processes of neurosecretion do not cease after spawning. Marchenko (1974, 1976a) described neurosecretory cells and phases of the neurosecretory cycle in the ganglia of the mussels, *Mytilus edulis* and *Crenomytilus grayanus*. The author gave a thorough review of works on the morphology of neurosecretory elements in Mollusca (1976b).

GERM CELLS, FERTILIZATION, EARLY EMBRYOGENESIS

Vassetsky (1973) describes in detail the dynamics of maturation divisions in the eggs of the giant oyster, *Crassostrea gigas*. Duration of the I-maturation division is approximately 1.5 times more than the duration of the II-maturation division (it must be added that these differences are considerably more prominent in vertebrates). Maturation divisions in unfertilized oyster eggs go up to the metaphase of the second division. Drozdov (1974) gives data on the ultrastructure of the spermium of the mussel, *Crenomytilus grayanus*. He finds a central canal which goes from the acrosomal region to the proximal centriole through the nucleus.

Ginsburg (1974a,b, 1975) notes the narrowness of optimal sperm concentration at fertilization in the bivalves, *Crassostrea gigas*, *Spisula sachalinensis* and *Mactra sulcata*. The maximal percentage of cleaving eggs was obtained at the sperm concentration 10^6 - 10^7 sperms/cm³. Increasing the concentration of the sperms leads to their slower activation, a decrease in their propulsion speed and some agglutination. Blyakher (1951) connects the formation of an antipolar lobe in the mussel with the nuclear movements.

MORPHOLOGY AND ECOLOGY OF LARVAE

The larval morphology of common species of Bivalvia

from the Black Sea is described by Zakhvatkina (1959, 1963, 1972), from the Caspian Sea by Galperina (1969) and from the Sea of Okhotsk by Kulikova (1975, 1976). Determinants for the identification of pelagic larvae of Bivalvia from the Black Sea (Zakhvatkina, 1959, 1972) are established for 25 species (18 families). All bivalve molluscs from the Black Sea are divided into three groups depending upon the pattern of their development. They are (1) those with complete pelagic development (the majority of the species), (2) those with incomplete pelagic development, when the development takes place in the mantle cavity up to the stage of the straight hinge (*Teredo navalis*, *Ostrea taurica*, *Montacuta bidentata* and *Barnea candida*), and (3) those with direct development through the formation of bottom-laying (*Loripes lacteus*, *Syndesmya ovata*).

Galperina (1959) identified the larvae of 5 species of Bivalvia from the Northern Caspian Sea by rearing them under laboratory conditions. Unlike the majority of investigators of the systematics of bivalve larvae, the author used the shell length/height/thickness ratio as the main diagnostic indicator. Kulikova (1975, 1976a,b) describes the larvae of common species of Bivalvia from the Busse Lagoon, Aniva Bay, Sea of Okhotsk. She describes the morphology and settlement of the larvae of *Musculista senhousia*. The larval morphology of the oyster, *Crassostrea gigas*, in the Possjet Bay, Sea of Japan, is given by Rakov (1974).

Nevesskaya (1960-1962) describes larval hinge structure and its ontogenetic changes. The author traces the hinge ontogenesis in more than 20 species of bivalve molluscs on the mass material from the bottom sediments of the Black Sea, stressing the absence of any connection between larval pro-vinculum and the adult hinge. The hinge of adult forms follows the stages of dental plates in the order Heterodonta and in the ostreids from the order Dysodonta.

PHENOLOGY AND DISTRIBUTION OF LARVAE

In the Black Sea, bivalve larvae are encountered in plankton almost all through the year, taking third or fourth place as to quantity of specimens per 1 m³. Seasonal fluctuations in the whole quantity of larvae coincide, in general, with water temperature changes, being maximum in number and diversity in summer. The larvae of *Mytilus galloprovincialis* are present in plankton all year. During August the larvae of all bivalve species are present (Kiseleva, 1965). In August when the wind blows toward the coast the number of bivalve larvae at the coastal zone becomes so high that the water becomes yellow (Dolgopolskaya, 1940). The presence of larvae throughout the aquatoria of the Black Sea, with the

most diversity in the coastal region, is noted by Kiseleva (1965).

Ivanov notes that the *Mytilus* larvae remain in upper water layers, which fall during heavy storms. Krakatitsa (1969) also draws attention to the fact that the layer of 0-5 cm is the richest one in oyster larvae, especially in veligers; in this layer their number may be as high as 18,000 specimens per 1 m³. Their quantity decreases sharply beyond depths of 45 cm. Began (1973) notes the high concentrations of larvae in the subsurface layer of Black Sea plankton; these concentrations may reach values of greater than 29,000 specimens per 1 m³. Vorobiev (1938) notes the adhesion of the *Mytilus* larvae to the surface film with the aid of the gas vesicle at stages just before metamorphosis.

The distribution and settling of *Teredo navalis* larvae in Gelenjik and Rybatskaya Bays of the Black Sea depend upon winds of northeastern direction. By turning surface water rich in larvae off shore, the wind causes an upwelling, which results in a decrease in the settling of larvae in this region (Ryabchikov, 1957).

In the Caspian Sea, up to the twenties, the larvae of Mollusca were relatively rare in the plankton (Hodkina, 1969, 1971). After *Mytilaster lineatus* moved into the Caspian Sea recently, its larvae took up a prominent position, and high biomasses of Bivalvia larvae, noted during the July-August period in the plankton of the middle and southern Caspian Sea (Hodkina, 1969), resulted from the presence of larvae of these species. The majority of bivalves from the Caspian Sea reproduce during the May-October period with a maximum quantity of larvae in the July-August period.

In the southern part of the Sea of Okhotsk (Southern Sakhalin) bivalve larvae are noted in the plankton during the July-October period with the maximum in August (about 15,000 specimens per 1 m³) (Kulikova, 1975). This high quantity of larvae resulted from synchronous spawning of common species of Mollusca. This spawning coincides with high (about annual maximum) water temperature, 18-22°C. The larvae of *Musculista senhousia* and some species from the family Tellinacea are predominant. During the August-October period the pelagic larvae of Bivalvia are second in quantity to Copepoda, and in July they hold the same position after Gastropoda.

INFLUENCE OF ENVIRONMENTAL FACTORS ON LARVAE

Kudinova-Pasternak (1962) reaches the conclusion that *Teredo navalis* is a eurythermic and euryhalinic species. Its distribution and activity, however, may be affected by

limiting values of salinity and temperature. Salinity of 8-9‰ is normal for adult forms; salinity of 12‰ is normal for larvae, while optimal temperature for larval development is 18-27°C. One can find similar data in the studies by Nikitin and Galajiev (1934), Zenkevich (1934), and Ryabchikov (1957). Ryabchikov, et al. (1963) state that the process of migration of teredinids into the Azov Sea occurs simultaneously with the increase in salinity. The fact that the highest salinity lies just above the lower border of values favorable for development of shipworms leads to a sharp decrease in the number of shipworms when the often observed slight lowering of salinity takes place. Thus, the authors conclude that the process of distribution of teredinids in the Azov Sea must be slow.

The influence of temperature and salinity regime on the larval plankton in the White Sea was shown by Pertsova and Sakhrova (1967). In 1966 the strong distillation and low water temperature caused by a very prolonged and severe winter had some influence on the reproduction and larval development of invertebrates. Bivalvia larvae were very scarce and only the larvae of *Macoma baltica* appeared at the normal times. At the end of the summer, only larvae of Mytilidae were in the plankton. All this, of course, affected the Bivalvia population structure for many subsequent generations and led to a decrease in the quantity of their larvae in plankton.

By comparing the data on reproduction and development of *Mytilus edulis* in the Black and White Seas, on the Atlantic coast of North America and on the Danish coast, Pale-nichko (1948) came to the conclusion that the duration of reproduction and development of *Mytilus* larvae is shortened in colder seas and is the shortest in arctic waters. The same fact was noted by Kulikova and Tabunkov (1974) with the development of the scallop, *Pecten yessoensis*, in the Sea of Okhotsk (Southern Sakhalin). In this region the duration of larval (pelagic) development is shorter than that in southern sections of the species area, and the average dimensions of larvae before settlement are smaller.

SETTLEMENT AND METAMORPHOSIS

The problems of settlement and metamorphosis are sufficiently studied in some species from families Teredinidae and Pholadidae.

Milyutina (1959) draws attention to structural and functional preparation for wood-boring in the shipworms during ontogenesis.

Kiseleva (1970) gives a detailed anatomy of the larvae of *Pholas dactylus* at the swimming-creeping stage during

metamorphosis and describes the behavior of the larvae. The author shows the high selectivity of the larvae to substratum. The larvae choose cracks and fissures in stones filled with silt and detritus. The high selectivity to substratum is shown for *Brachyodontes lineatus* (Kiseleva, 1966b). The stimulating metamorphosis factor for this species is the soluble organic substance excreted by algae. Bacterial-algal film covering solid substrata is also a trigger of metamorphosis. Belogrudov (1973, 1974) points out the necessity for a bacterial-algal film on the collectors for successful settlement of the scallop larvae, *Pecten yessoensis*. Under natural conditions, the best substratum for settlement is the alga *Ceramium kondoi* (Belogrudov, 1973).

Petukhova (1963), Gorin (1969, 1970), Zevina (1972) and other authors describe the phenology of settlement of the larvae in the seas of the USSR.

Thus, Soviet authors presently study such various aspects of the reproduction of Bivalvia as gametogenesis and reproductive cycles (morphological and ecological aspects), neurosecretory regulation of the reproductive cycles, fertilization and early embryogenesis, larval development, phenology of the larvae, influence of environmental factors on the gametes and larvae, metamorphosis and settlement of the larvae, and the ecology of these processes.

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REPRODUCTIVE CYCLES OF *STYELA PLICATA*

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In estuaries of the southeast U.S., the solitary tunicate, *Styela plicata*, is a common suspension-feeding organism. Near Beaufort, N.C., the approximate northern limit of its occurrence, cycles of larval settlement of this species have been observed. Larvae settle heavily in spring and fall, but only lightly in summer and winter. Previous ecological experiments had suggested that neither competition nor predation were responsible for the low settlement of larvae in summer, and that the basis for the cycles might be physiological in origin. Therefore, experiments were designed to test the validity of several physiological hypotheses.

To test the hypothesis that the low larval settlement in winter and summer is due to low food abundance, the particulate matter of the Newport River estuary near Beaufort, N.C. was sampled for one year. However, neither quantity nor qualitative composition of the particulate matter could be correlated with the observed larval settlement.

To test the hypothesis that metabolic maintenance costs or physiological partitioning of resources might be poorly adapted at the extremes of temperature in summer and winter, carbon and nitrogen budgets were constructed for *Styela*. However, metabolic maintenance costs were estimated to require only 18% of the carbon and 37% of the nitrogen available for metabolic processes; and, furthermore, growth and an estimate of reproductive potential were maximal at summer temperatures.

After reexamining the original assumptions, it was found that the estimate of reproductive potential provided an approximate reconstruction of the observed larval recruitment when adult population size and predation intensity were considered. It is concluded that neither food abundance nor metabolic maintenance costs can explain low periods of larval settlement. Predation on larvae and young adults appears to be responsible for the low rate of settlement observed in summer months.

HEAVY METAL EFFECTS ON REPRODUCTIVE SUCCESS
IN MARINE BIVALVES

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Heavy metals have long been recognized as serious pollutants of the marine environment. In recent years considerable research effort has been placed on determining the effects of these metals on marine organisms. Relatively little is known, however, about metal effects on invertebrates, especially their embryonic and larval stages. This presentation describes some findings of the Milford Laboratory on the effects of an array of metals on embryonic and larval marine bivalves. Experiments were conducted to determine the acute toxicity and mutagenic effect of metals on development of embryos of the American oyster, *Crassostrea virginica*. Toxicity studies were also conducted with the hard clam, *Mercenaria mercenaria*. Further studies were completed to determine the survival rate and growth response of larvae of the American oyster exposed to metals.

The acute toxicity of 11 heavy metals to embryos of the oyster was studied and the concentrations at which 50% of the embryos did not develop were determined. The most toxic metals and their LC₅₀ values were mercury (0.0056 ppm), silver (0.0058 ppm), copper 0.103 ppm and zinc (0.31 ppm). Those metals that were not as toxic and their LC₅₀ values were nickel (1.18 ppm), lead (2.45 ppm) and cadmium (3.80 ppm). Those metals that were relatively non-toxic and their LC₅₀ values were arsenic (7.5 ppm), chromium (10.3 ppm) and manganese (16.0 ppm). Aluminum was non-toxic at 7.5 ppm, the highest concentration tested.

In conjunction with the above studies the effects of four metals on the cyto-genetics of fertilization, meiosis and cleavage were determined. Silver and cadmium reduced the number of mitoses at the 0% kill level, while also causing division abnormalities and irregularities. Arsenic caused abnormalities in the latest stage zygotes at the 100% kill level. Manganese caused severe direct changes in the ploidy level of zygotes, and in losses of pieces and of

whole chromosomes.

The acute toxicity of 5 metals to clam embryos was also determined. The most toxic metals and their LC₅₀ values were mercury (0.0048 ppm) and silver (0.021 ppm). Zinc and nickel, although not as toxic as mercury and silver, had LC₅₀ values of 0.166 and 0.31 ppm. Lead was the least toxic with an LC₅₀ value of 0.78 ppm.

A logical extension of the previously described studies was to determine the effect of some of these same metals on larvae of these bivalves. A study on oyster larvae from 2 to 12 days of age has been completed. Mercury, silver and copper are the most toxic, while zinc and nickel, the least toxic.

REPRODUCTION AND DISPERSAL IN MARINE
BENTHIC INVERTEBRATES

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Three of the most common developmental patterns in marine benthic invertebrates are planktotrophy in which initially small larvae undergo an extended pelagic feeding and growing period prior to metamorphosis, pelagic lecithotrophy in which the somewhat larger free-swimming larvae subsist entirely on stored yolk until metamorphosis, and benthic development in which the non-feeding larvae remain in the benthos throughout larval life. A fourth somewhat less common developmental type consists of a long prefeeding benthic period followed by a very short larval planktonic feeding existence. Which larval pattern is likely to evolve in particular cases depends on two classes of selection pressures: those which influence production and survival of larvae, and those which affect survival after metamorphosis. This paper presents the results of a mathematical model which attempts to define conditions under which each reproductive pattern is optimal.

Evolution of the three more common patterns may depend only on the properties of the larval environment. Assume the following: (1) the length of the larval prefeeding and feeding periods increase and decrease linearly with egg size, respectively; (2) development of feeding larvae is faster when food is abundant; and (3) planktonic and benthic mortality rates are constant and perhaps different. The following conclusions emerge: (A) when planktonic food is abundant and planktonic mortality low, planktotrophic larvae with a long feeding period should evolve; (B) when planktonic food is rare and planktonic mortality low, pelagic lecithotrophic larvae should evolve; and (C) when benthic mortality is lower than planktonic mortality, benthic development should evolve. It is to be emphasized that pelagic larval existence may arise whether or not larval dispersal is advantageous.

Evolution of those larvae with brief planktonic

existence may result from selection for dispersal ability. Assume the following: (4) the species is divided into many local populations with identical demographic characteristics between which migration via planktonic larval dispersal can occur; (5) each population independently is subject to random, density-independent adult mortality; and (6) the probability that a planktonic larva born in a local population metamorphoses in that same population decreases exponentially with time in the plankton. Under such circumstances, the model predicts that: (D) a long pelagic larval feeding period may evolve even though planktonic food is not particularly abundant or planktonic mortality particularly low; or (E) a short planktonic period following prolonged non-feeding benthic existence may arise as a compromise between efficient juvenile production via benthic development and maximum post-metamorphosis survival resulting from dispersal.

Whether larval production and survival on the one hand or dispersal and post-metamorphosis survival on the other play the dominant role in evolution of marine invertebrate reproductive patterns remains unclear. What does seem clear is that each is important in specific cases: selection for larval production is probably responsible for the planktotrophic larvae of those species whose adult populations remain essentially constant, while selection for dispersal probably produced those larvae with quite brief planktonic periods.

LIFE HISTORIES AND THE DYNAMICS OF FOULING COMMUNITIES

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INTRODUCTION

An emerging paradigm of marine benthic community organization postulates the existence of competitive hierarchies in which one or a few species "wins" in the absence of disturbances (Connell, 1970, 1972, 1975; Dayton, 1971, 1975; Dayton, *et al.*, 1974; Fishelson, 1973; Menge and Sutherland, 1975; Paine, 1966, 1971, 1974; Paine and Vadas, 1969; Porter, 1972, 1974; Woodin, 1974). Competition is generally for space (Connell, 1972) or space and light (Dayton, 1975). This process is often counteracted by preferential predation on the dominant competitor (e.g., Paine, 1966) or by some more generalized physical disturbance (e.g., Fishelson, 1973). These latter processes generally result in the co-existence of an increased number of species because the competitive dominant is prevented from "winning". However, predation and physical disturbances can also be so intense as to reduce species richness directly (Dayton, 1971; Paine and Vadas, 1969).

In spite of the convincing application of this paradigm to a variety of marine systems, one marine community generally seems to lack a competitive dominant. This is the community of sessile organisms associated with the fouling of man-made structures, but which also occurs on other hard substrate subtidally (WHOI, 1952). It is most often a complex mixture of hydrozoans, bryozoans, sponges, and tunicates. In the absence of (obvious) predators and physical disturbances, temperate and subtropical fouling communities undergo continual and drastic changes in species composition

(Boyd, 1972; Cory, 1967; Fager, 1971; Haderlie, 1968; Karlson, 1975; Kawahara, 1962; McDougall, 1943; Millard, 1952; Ralph and Hurley, 1952; Smith, *et al.*, 1950; Sutherland, 1974, 1975; Sutherland and Karlson, 1973 and in preparation; Wells, *et al.*, 1964a). With a few notable exceptions, no single species seems capable of monopolizing space for extended periods of time (i.e., for many years).

Logically, a competitive dominant would be a species with an "ideal" space utilization strategy. It would have a continuously high recruitment rate; it would be able to invade and occupy previously occupied substrate; and it would live for many years. The last point implies not only longevity, but also a highly developed ability to prevent subsequent invasions and epizooic overgrowth. Short of this ideal, competitive domination could conceivably be achieved by an organism possessing any two of the three "ideal" characteristics. A high recruitment rate coupled with an ability to invade occupied substrate would obviate the necessity for a long life span. The competitive dominant would just have a high turnover rate. A long-lived animal with a high recruitment rate could gradually occupy all available space even if the larvae were poor invaders of occupied space. The high recruitment rate would increase the probability of successful invasions, and once settled, the adult would be "permanent". Finally, a long-lived organism could dominate the community even with a low recruitment rate if the larvae were highly successful invaders of occupied substrate.

In what follows I summarize some data on recruitment rate, ability to invade occupied substrate, and longevity, in an attempt to discover which part of the life cycle is "responsible" for the absence of a competitive dominant in this community. No attempt is made here to thoroughly review the prodigious amount of literature on this subject, but I believe the data generally are characteristic of temperate and subtropical fouling communities.

Recruitment: I have chosen four studies in which recruitment data are available for at least two years to illustrate what appears to be an extraordinary amount of variability in larval recruitment. Two of these studies were conducted on the west coast of North America at Bodega Bay, California (Boyd, 1972), and La Jolla, California (Coe and Allen, 1937) while the other two were carried out on the east coast at Beaufort, North Carolina (Sutherland and Karlson, in preparation) and Biscayne Bay, Florida (Weiss, 1948 a). Data were taken from graphs (Coe and Allen, 1937; Weiss, 1948 a) or tables (Boyd, 1972; Sutherland and Karlson, in preparation) and the coefficient of variation (Sokal and Rohlf, 1969) was calculated for the recruitment of each species or species group throughout

the observation period (Table 1).

In each study the amount of variation in recruitment rate was extremely high, usually exceeding 100% (Table 1). This reflects not only seasonal variation in recruitment, often there are months without significant recruitment of a species, but variation from year to year during comparable time periods. There is no convincing evidence that the variation is higher on the east coast, in spite of the greater variability in temperatures on this coast. The range in Beaufort is almost 25°C (Sutherland and Karlson, 1973) while the range at Bodega Bay is only about 5°C (Sutherland, 1970). There is also no clear correlation with latitude.

Whatever the reason for this variation, it makes it impossible to predict what larvae will be in the plankton at any given time. This is borne out by the variability in initial development of newly submerged substrate (e.g., Sutherland and Karlson, 1973 and in preparation; Boyd, 1972) and will become important in the discussion that follows.

Recruitment to previously occupied substrate: Except for some anecdotal references on the effect of resident adults on larval recruitment (e.g., Weiss, 1948 b), Boyd (1972) was the first to attempt a rigorous analysis of this process. His experimental design included long-term, nondestructive censuses of species composition on sequentially submerged substrate. As a result he was able to compare larval recruitment on substrates submerged for different periods of time, with different densities of resident adults, over the same four week period. Some of his results are reproduced in Table 2. In all cases except one, recruitment was generally heaviest on the "youngest" plates, those submerged from four to eight weeks. Boyd (1972) concluded that most species "preferentially settled on essentially clean substrates". The one exception was *Botrylloides* sp. which occurred sporadically throughout his observation period and settled equally well on occupied and unoccupied space.

Boyd's results clearly indicate that resident adults inhibit subsequent larval recruitment, although they usually did not stop it entirely. However, he did not report which resident adults were doing the inhibiting and whether or not different species were differentially capable of preventing subsequent recruitment. I have made observations of this kind on sequentially submerged, non-destructively sampled substrate at Beauford, North Carolina (Sutherland and Karlson, 1973 and in preparation). Since only percent cover data were taken in my study, it was necessary to wait until a species (=species 1) became abundant enough to cover a substantial portion of a plate in order to detect its presence. A period of 90 days was

Table 1.

Coefficient of Variation in Recruitment Rate on Artificial Substrate Submerged for Short Periods of Time. Data from Bodega Bay (Boyd, 1972), La Jolla (Coe and Allen, 1973), Beaufort (Sutherland and Karlson, in preparation), and Biscayne Bay (Weiss, 1948a).

	Feb 1969- Feb 1971		Apr 1971- Dec 1974
<i>Obelia</i> spp.	101	<i>Tubularia</i>	223
<i>Balanus</i>		<i>Pennaria</i>	266
<i>crenatus</i>	145	<i>Schizoporella</i>	168
<i>Bowerbankia</i>		<i>Bugula</i>	197
<i>gracilis</i>	163	<i>Styela</i>	212
<i>Schizoporella</i>		<i>Ascidia</i>	161
<i>unicornis</i>	100	<i>Botryllus</i>	361
<i>Cryptosula</i>		<i>Haliclona</i>	319
<i>pallasiana</i>	73	<i>Halichondria</i>	362
<i>Bugula</i>		<i>Balanus</i>	150
<i>californica</i>	209	<i>Ostrea</i>	203
<i>Bugula</i>			
<i>neretina</i>	332		
<i>Alcyonidium</i>			
<i>polyoicum</i>	197		
<i>Ascidia</i>			
<i>ceratoides</i>	277		
<i>Botrylloides</i>			
sp.	136		
<i>Botryllus</i>			
sp.	336		
Bodega Bay, California #/100cm ² after 4 weeks			
Beaufort, North Carolina #/m ² /day during 3 weeks			
	Dec 1932- Oct 1935		Sep 1942- May 1946
<i>Ectocarpus</i>	78	<i>Hydroids</i>	
<i>Herpsiphonia</i>	226	(% cover)	281
Diatoms	81	<i>Tunicates</i>	
Hydroids	126	(% cover)	100
Barnacles	173	<i>Anomia</i>	301
Oysters	196	<i>Tubeworms</i>	174
Bryozoa	149	<i>Bugula</i>	154
Serpulids	302	<i>Encrusting</i>	
Amphipods	173	<i>Bryozoans</i>	144
		<i>Barnacles</i>	88
La Jolla, California Rel. Vol. after 8 wks			
Biscayne Bay, Florida # or % cover/500 cm ² after 1 month			

Table 2.

Effect of Previous Occupants on Larval Recruitment. Values in table are mean # of individuals/100 cm² after 4 weeks (n=5). Comparisons were made by means of ANOVA (Sokal and Rohlf, 1969). From Boyd (1972).

	Time of Analysis	Weeks of Exposure					Significance level
		4	8	12	16	F _s	
<i>Balanus crenatus</i>	Sep 69	146	288	26	2	28.7	.001
<i>Obelia</i> spp.	Dec 69	46	3	3	8	12.1	.001
<i>Ascidia ceratodes</i>	Jul 69	20	164	23	23	11.8	.001
<i>Bugula californica</i>	Nov 69	387	36	10	80	20.1	.001
<i>Cryptosula pallasiana</i>	Jul 69	39	43	0	0	8.8	.001
<i>Botrylloides</i> sp.	Sep 69	39	28	20	20	2.3	NS
<i>Schizoporella unicornis</i>	Jun 69	24	30	28	4	5.3	.001

arbitrarily taken as adequate. At the end of that time, the percent cover of species 1 was compared to the percent cover of species 1 on a previously submerged plate which had been monopolized ($> 80\%$ cover) by species 2 over the 90 day interval in question. Differences in percent cover for species 1 were assumed to result from the inhibition of recruitment and/or growth by species 2.

Although Table 3 is a necessarily incomplete cataloguing of those chance occurrences which satisfy the above conditions, it is apparent once again that residents strongly inhibit recruitment and/or subsequent growth. What is of particular interest is that many of these relationships are reciprocal. For example, *Schizoporella* inhibited the recruitment and/or growth of several species, but was itself unable to invade areas occupied by these same species. These reciprocal interactions mean that the order of invasion has an important effect on subsequent community development (see also Sutherland 1974).

Other observations at Beaufort (Sutherland and Karlson, 1973, in preparation) indicate that some species are better able to inhibit subsequent larval recruitment than others. For example, *Hydractinia echinata*, an encrusting hydroid, has occupied one plate for three and one half years, resisting essentially all larval recruitment during that time. On the other end of the scale, oysters and barnacles (unless the latter are very dense) are usually overgrown by new recruits in a few months.

The larvae of some species are also better able to invade than others. For example, *Styela plicata* commonly invaded mixed assemblages of adults from 1972-1974, and in December 1974 many previously occupied plates were invaded by *Botryllus* (Sutherland and Karlson, in preparation). The sponges, *Halichlona*, and *Halichondria*, are also good invaders of occupied substrates at Beaufort (loc. cit.). Finally, we have already seen that *Botrylloides* sp. is capable of invading adult assemblages at Bodega Bay (Table 2).

Except for the few species like *Hydractinia* at Beaufort, or *Aurelia schyphistomae* at Bodega Bay (Table 4) no resident assemblage is completely invulnerable to larval recruitment. *Schizoporella unicornis* at Beaufort is one of the most highly resistant species to subsequent larval recruitment (Sutherland, 1975). Nonetheless, species are gradually added to *Schizoporella* monopolies. For example, three plates submerged at Beaufort in August 1971 were monopolized by *Schizoporella*, yet diversity gradually increased with time (Fig. 1).

Table 3.

Effect of Resident Species (on left) on the Recruitment and/or Growth of New Recruits (across top). In each pairwise comparison, the top number(s) are estimates of percent cover for the recruit after 90 days on plates dominated (>80% cover) by the resident during that period. The bottom numbers are estimates of percent cover for the recruit in newly submerged plates after the same 90 day period.

Resident	Recruit				
	<i>Tubularia</i>	<i>Penaria</i>	<i>Bugula</i>	<i>Schizoporella</i>	<i>Ascidia</i>
<i>Hydractinia</i>	0	0	0	0	0
	8,21,21,23	26,29,25,41	29,53,48,68	69,52,55,65	39,47,17,21
<i>Schizoporella</i>	20,5,13	0,0,0,1	12,14,23,13		11,14,0,9
	39,55,38	26,29,25,41	29,53,48,68		48,23,28,24
<i>Styela</i>	3,3,12		0,0,0	1,2,0	0,0,0
	60,63,86		37,47,44	50,78,89	82,65,83
<i>Ascidia</i>			4,2,5		1,0,0
			34,47,44		82,65,83
<i>Balanus</i>	10,1,1		1,3,4		
	39,55,38		34,47,44		

* = after one month

Table 4.

Longevity.

Bodega Bay Data from Boyd (1972, Table 13). Life cycle length = longevity of an individual. Beaufort data from long-term, nondestructive censuses of artificial substrates (Sutherland and Karlson, in preparation). Residence time may be greater than individual life spans if replacement occurs.

Bodega Bay, California		Beaufort, North Carolina	
	Life Cycle Length (years)		Maximum Median Residence Time (years)
<i>Obelia</i> spp.	0.2	<i>Halichondria</i>	0.7
<i>Balanus crenatus</i>	0.8	<i>Haliclona</i>	0.8
<i>Bugula californica</i>	0.5 - 0.7	<i>Hydractinia</i>	indefinite
<i>Bowerbankia gracilis</i>	0.3 - 0.4	<i>Pennaria</i>	0.6
<i>Schizoporella unicoris</i>	0.3 - 0.5	<i>Tubularia</i>	0.7
<i>Cryptosula pallasiana</i>	0.3 - 0.5	<i>Bugula</i>	0.8
<i>Ascidia ceratodes</i>	0.5 - 0.7	<i>Schizoporella</i>	2.5
<i>Botrylloides</i> sp.	0.2 - 0.3	<i>Ascidia</i>	0.4
<i>Aurelia labiata</i> (Schyphistoma)	indefinite	<i>Styela</i>	1.2
		<i>Botryllus</i>	0.4
		<i>Ostrea</i>	0.8
		<i>Balanus</i>	1.0

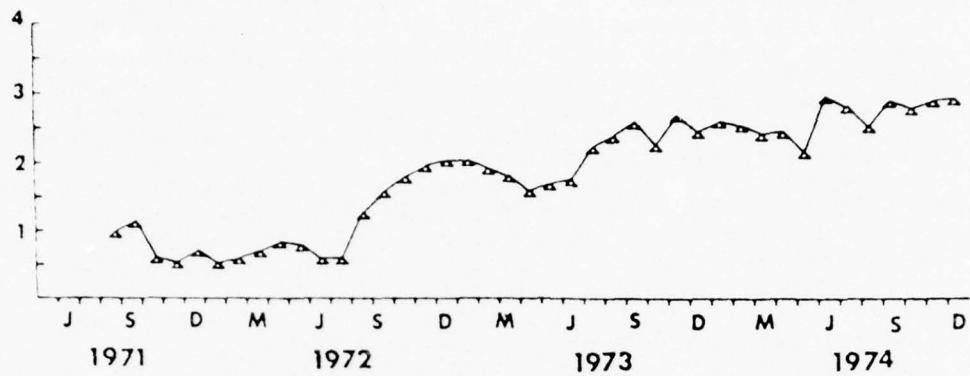


Fig. 1. Brillouin index of diversity calculated for the average species composition of 3 plates submerged in August 1971 and dominated initially by *Schizoporella*.

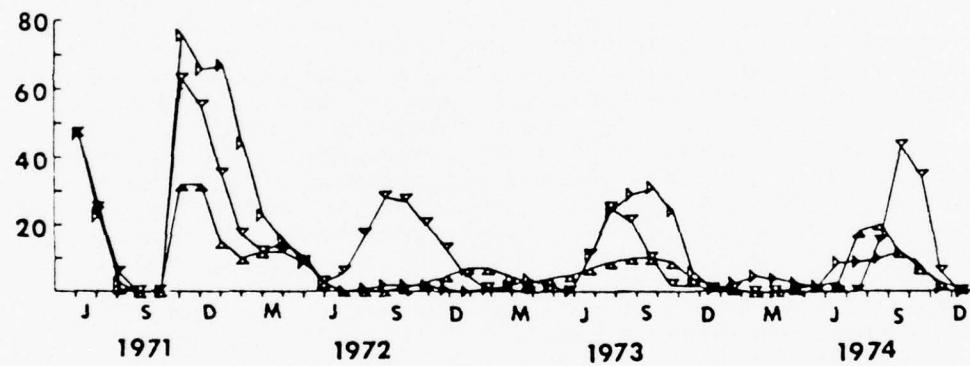


Fig. 2. Percent empty space present on 3 undisturbed plates submerged in May 1971. Δ = plate 1, ∇ = plate 2, \blacktriangleright = plate 3.

It is thus clear that resident assemblages inhibit subsequent larval recruitment and that many of these interactions are reciprocal. It is also clear that different species are differentially capable of resisting larval recruitment as adults and of invading adult assemblages as larvae. Thus the successful invasion of an adult assemblage is a highly complex matter depending on the species composition of that assemblage and the species composition of the larvae in the plankton.

Longevity: Data on this aspect of the biology of these organisms are rare because most sampling regimes are destructive in nature. Two studies which include data on longevity are those of Boyd (1972) at Bodega Bay, and my own studies at Beaufort (Sutherland and Karlson, 1973 and in preparation.) In both cases information is based on repeated, nondestructive censuses of the same substrates.

Clearly most of the dominant organisms on both coasts are short-lived, even allowing for the possible overestimation of longevity at Beaufort (Table 4). Life spans of four to eight months are common. In each area, however, there appears to be one species capable of persisting for an indefinite period of time. This persistence implies not only longevity, but an ability to prevent subsequent larval recruitment.

These short life spans contribute to the spontaneous "slough-offs" which are often associated with the mortality of the dominant organisms. Organisms which are attached to the dying species disappear with it. In some cases slough-offs can occur when apparently healthy organisms become detached from the substrate. This occurs commonly with solitary tunicates at Beaufort, organisms which are capable of settling in mixed species assemblages. Often the site of attachment is initially precarious, being on top of other organisms rather than on primary substrate. Although the attachment site may serve while the tunicate is small, it eventually becomes too large and is dislodged along with the original occupant by tidal currents. This can happen with many individuals simultaneously and can be a catastrophic event leaving behind much free space.

Whatever their cause, slough-offs at Beaufort commonly occur in the fall and can result in the provision of 20-60% clear substrate (Fig. 2). Similar events have been observed in fouling communities in California (Boyd, 1972; Haderlie, 1968; Fager, 1971), Japan (Kawahara, 1962), New Zealand (Ralph and Hurley, 1952) and South Africa (Millard, 1952).

DISCUSSION

If we now ask which part of the life cycle is "responsible" for the absence of a competitive dominant in this community, the answer for most species is "all three parts". The majority of the species discussed here have extremely variable recruitment, have difficulty invading previously occupied substrate, and are short-lived. The longest-lived organisms, e.g., *Hydractinia* at Beaufort and *Aurelia schyphistomae* at Bodega Bay (Table 4), "almost never" reproduced. At Beaufort we have observed only five or six colonies of *Hydractinia* in four years of following several hundred plates. The same low level of recruitment was true for *Aurelia schyphistomae* at Bodega Bay (Boyd, 1972). Additionally these species seem incapable of invading occupied substrate; all but one of the *Hydractinia* colonies observed at Beaufort were epizooic and disappeared along with the original occupant. *Schizoporella* at Beaufort has a high, but variable recruitment rate and colonies persist for a moderately long time (Table 4), but it is such a poor invader of occupied substrate it gradually disappears from undisturbed communities (Sutherland, 1975). *Styela* is the only other possibility at Beaufort, having a moderately long life (Table 1) and being able to invade occupied substrate. However, when this solitary tunicate becomes dense enough to exclude other community members, the resulting, anastomozing mats of individuals become unstable and slough off (Sutherland and Karlson, 1973; Sutherland, 1974). The longest-lived individuals are solitary.

In the absence of disturbance there are periods when one or more of the "good invaders" (e.g., solitary and colonial tunicates and sponges) is dominant, occupying greater than 50% of the area (e.g., Boyd, 1972; Karlson, 1975; Sutherland and Karlson, 1973, in preparation). However, this dominance does not last because the organisms are short-lived or conversely because their recruitment rates are so low. I conclude in general that there is no competitive dominant in temperate and subtropical fouling communities. The absence of such a dominant represents a fundamental difference between this community and other well known benthic marine communities (Dayton, 1971, 1975).

While certain species can impart some degree of stability to the community by persisting for considerable lengths of time and by resisting larval invasion (I have called these patches multiple stable points (Sutherland, 1974)), over a period of several years species are usually added as a result of larval recruitment (e.g., Fig. 1). Additionally, short life spans contribute to more or less annual, catastrophic slough-offs which result in the provision of substantial amounts of free space (e.g., Fig. 2). We have seen

that free space is the preferred site for subsequent larval recruitment (Table 2). Indeed, sequential observations of substrate at Beaufort have indicated that free space produced by slough-offs has usually been colonized by new recruits rather than being filled in by the expansion of resident colonies (95% of the time, $n = 42$). We have also seen that variability in larval recruitment is high. Thus we cannot predict which larvae will be added to resident assemblages or to the free space made available by catastrophic slough-offs. However, observations at Beaufort have shown that the species settling in the free space is usually a different species than the original occupant (82% of the time, $n = 39$). The subsequent development of this free space depends on the ability of the new resident to resist subsequent recruitment and the identity of the larval recruits. Thus variable recruitment, differential ability to invade occupied substrate, and short life spans all work together to produce a community with no stable climax of the "usual" sort (e.g., Odum, 1969). Change is the rule rather than the exception in fouling communities all over the world, in North Carolina (Carlson, 1975; McDougall, 1943; Sutherland, 1974, 1975; Sutherland and Carlson, 1973, in preparation), Florida (Smith, *et al.*, 1950), California (Boyd, 1972; Haderlie, 1968; Fager, 1971), Japan (Kawahara, 1962), New Zealand (Ralph and Hurley, 1952), and South Africa (Millard, 1952).

Terrestrial plant communities are traditionally thought to respond to perturbations (e.g., fires) with a community controlled process called succession (Odum, 1969). In at least some of these communities, viable seeds of successional species are present in the soil and germinate immediately after the climax species are removed (Marks, 1974). These successional species "prepare the way" for the development of the climax community. In contrast the fouling community has no such reservoir of "successional" species. Colonization is generally by animals which have short-lived, even nonfeeding larvae (Barnes, 1968). Instead of "preparing the way" for subsequent larval recruitment, residents often inhibit it. Finally, the process of community development, e.g., on unoccupied substrate, usually does not produce a stable climax. Thus fouling communities provide little evidence in support of the traditional view of succession (e.g., Odum, 1969).

In all benthic communities, larval recruitment represents the major process by which the community responds to perturbations, but at the same time constitutes a potential perturbation to existing adult assemblages. I believe future research should focus on the ability of larvae to invade previously occupied substrate and on the mechanism by which the resident adults inhibit this invasion. In

addition, studies should be conducted which, whenever possible, involve long-term, nondestructive censuses of the same sites. Only in this way can the essential life history information be gathered on the community members, and only in this way can questions related to community stability be answered. Finally, the roles of important community members can only be determined through the experimental manipulation of their density, e.g., excluding important predators or removing important competitors.

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ECOLOGICAL IMPLICATIONS OF PATTERNS OF ROCKY INTER-TIDAL COMMUNITY STRUCTURE AND BEHAVIOR
ALONG AN ENVIRONMENTAL GRADIENT

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INTRODUCTION

In seeking to understand local and geographic patterns of community structure and behavior, most ecologists have relied on examination and comparison of such patterns. Though these techniques will always remain an integral part of the fabric of ecological research, ecologists are becoming increasingly aware of the equivocal nature of conclusions based exclusively on an observational-comparative approach. Luckily, increasing numbers of ecologists realize that the best way to reduce such uncertainty is through the performance of controlled, replicated field experiments (e.g. Connell, 1975a,b; Dayton, 1971, 1975a; B. Menge and Sutherland, 1975; Paine, 1974; Schroder and Rosenzweig, 1975). At present the primary practitioners of this approach are marine and plant ecologists, perhaps because the organisms they study are largely slow moving or sessile and readily manipulated. In my opinion, some of the most exciting advances in our understanding of community-level patterns have emerged over the past fifteen years from experimental field studies in these systems.

Early work in community ecology established the existence of certain recurrent patterns of distribution, abundance, size, trophic structure, species diversity and community development; i.e. various patterns of community "structure" were observed. Current research is aimed primarily at understanding the dynamics of communities; i.e. how an observed community structure arises and persists. An especially intriguing and controversial focal point has been the problem of understanding why certain areas of the globe have many more species than others. More specifically, ecologists have tried to explain the relative effects of several factors (e.g. predation, competition, climatic stability, productivity, spatial heterogeneity, time,

temporal heterogeneity - see Pianka, 1966, 1974) on patterns of within and between habitat species diversity (MacArthur, 1964, 1969). A recent synthesis by B. Menge and Sutherland (1975), considered in some detail below, suggests local species diversity is maintained primarily by the relative overall (community-wide) intensity of predation and competition, which are inversely related. These are in turn influenced by climatic stability, temporal heterogeneity, structural heterogeneity, productivity, and perhaps other factors. Sutherland and I further suggested that decreasing environmental rigor permitted the development of an increasingly complex trophic structure. When trophic structure is complex (e.g. many trophic levels, many connections between component species), predation is intense and is the dominant structuring agent in the community. In trophically simpler communities overall predation intensity lessens and the role of competition in structuring the community increases. This synthesis is supported by experimental data from several habitats (e.g. Connell, 1961a, 1970, 1971, 1975b; Dayton, 1971, 1975a; Jackson, 1972; B. Menge, 1972b, 1976; Paine, 1966, 1971, 1974; Woodin, 1974).

A second even more controversial problem has been trying to understand differences in community "stability" among similar kinds of habitats (e.g. rocky intertidal region, forests, deserts, lakes, etc.) experiencing different regimes of environmental stability (e.g. see Woodwell and Smith, 1969). The latter question has been especially problematic because "stability" can be defined in numerous quite different but equally significant ways (Holling, 1973; Margalef, 1969). A major, but as yet poorly quantified, global pattern of community "stability" seems to be that tropical communities are more persistent (i.e. exhibit less variation over time) but have less resilience (Holling, 1973) or adjustment stability (Margalef, 1969) than do more poleward communities (but see Peterson, 1975, for qualifications).

In this paper, I examine these two problems (species diversity and community stability) and suggest qualitative models explaining patterns of community organization and community stability. These models are in many ways tentative and speculative, but rest nonetheless on what I feel to be a firm foundation of largely experimental field analyses of community structure. This paper, though an "overview" of experimental community ecology, is not a review in the strict sense. Quite adequate reviews have recently appeared elsewhere (Connell, 1972, 1975a,b; B. Menge and Sutherland, 1975). Rather, my goals here are to concentrate on general concepts with reference to relevant publications when appropriate. Some data from my studies on rocky intertidal community organization in New England are included to illustrate my points.

COMMUNITY STRUCTURE AND ORGANIZATION ALONG ENVIRONMENTAL GRADIENTS

Definitions

Despite the sometimes overwhelming confusion in the literature, few critical concepts in ecology have a single widely accepted definition. As a result, such terms as competition, community, predation, etc., must be redefined with each use. The definitions I have in mind when using such terms in this paper are given in Table 1. These are taken from several sources (Dayton, 1971, May 1973; B. Menge, 1976; B. Menge and Sutherland 1975, Pianka, 1974, Reynoldson and Bellamy, 1971, Root, 1967).

Causes of Community Structure in Hard Bottom Marine Systems

Modern science has progressed primarily by an interplay between analytic and synthetic techniques, the goal being to build an understanding of complex systems by an understanding of the behavior of its components and how these interact to produce the observed system. Hence the eventual development of a global model or cluster of models of community organization should rest on syntheses suggested by analyses of local communities arrayed along local environmental gradients. Subsequent comparison between such systems should reveal which generalizations are restricted to local situations and which can be broadened to higher levels of complexity to explain widely observed patterns.

The fact that some areas have relatively many species (e.g. tropical forests, coral reefs, deep-sea soft sediment communities, etc.) and others have relatively fewer (e.g. temperate forests, kelp forests, shallow-sea soft sediment communities, etc.) is, of course, widely realized (e.g. see MacArthur, 1969, 1972; Ricklefs, 1973). Although the generation of species and thus species diversity results from poorly understood speciation processes, the maintenance of varying levels of species diversity is clearly some function of interactions between characteristics of the biological and physical environment. In my view, the biological interactions of predation (including herbivory), biological disturbances caused by the activities of a species, and competition are the cardinal factors regulating local species diversity. Other factors such as structural and temporal heterogeneity, production, etc., have modifying effects and may affect diversity both directly and indirectly through their effects on predatory or competitive interactions (B. Menge and Sutherland, 1975).

Recently, Sutherland and I suggested a simple model

Table 1. Definitions of ecological terms used in text.

Term	Definition
Predation	Consumption of one species by another. Can refer specifically to carnivory or more generally to include consumer-prey interactions (excluding parasitism).
Interspecific Competition	Mutual striving by two species for a resource or resources in short supply. Both species are negatively affected in this interaction.
Guild	Assemblage of species in a community of comparable trophic status or which utilize similar spatial resources.
Community	Directly or indirectly interacting assemblage of species occupying a particular habitat. Includes all trophic levels.
Species Diversity	Number of species in a community (=species richness).
Community Structure	Collective expression referring to the "appearance" of a community; quantifiable only by quantifying distribution, abundance, body size, trophic relationships, and species diversity of component populations.
Community Organization	Community structure and the dynamic processes responsible for the observed structural patterns.
Environmental Stability	Variation of parameters of the physical environment.
Environmental Predictability	The probability of predicting the future status of parameters of the physical environment. Measured by (e.g.) serial auto-correlation of these parameters.
Environmental Stress	Frequency that physical environmental conditions approach or exceed the physiological tolerance limits of an organism.
Environmental Rigor	A more general term meant to include the three above characteristics.
Temporal Heterogeneity	Environmental rigor plus patterns and levels of production.

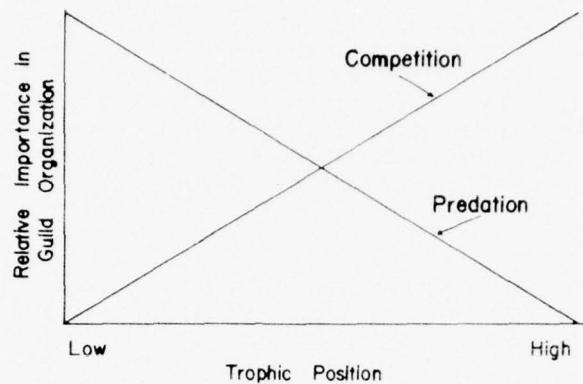
to explain the seemingly contradictory (e.g. Pianka, 1966) effects of competition and predation on species diversity in a community. Summarizing what are actually rather complex hypotheses, the predation hypothesis suggests that selective predation on competitively dominant species maintains high species diversity by alleviating competition and permitting the invasion and persistence of otherwise inferior competitors (e.g. Paine, 1966). Predation intensity increases with increased environmental stability because predator activity and diversity increases in such environments. Various portions of this hypothesis are supported by evidence from field experiments (e.g. Hall, et al., 1970; Paine, 1966, 1971; see B. Menge and Sutherland, 1975, for additional references).

The competition hypothesis argues, on the other hand, that with increased environmental stability, competition intensity increases because species can devote more time and energy to resource acquisition (and less to coping with the physical environment) (MacArthur and Wilson, 1967). Intense competition results in increased specialization and higher species diversity (MacArthur, 1972). Evidence supporting this hypothesis is mostly of an indirect, correlative nature; see B. Menge and Sutherland (1975) for references and a more detailed summary of these hypotheses.

Fig. 1 (from B. Menge and Sutherland, 1975) suggests how these hypotheses may be combined into a simple model which reconciles the apparent contradictions between them. The basic points of the model are that within a community, (1) competition regulates species number in a guild only when the members of that guild actually compete, i.e. when they are at or near carrying capacity (K). This is usually true at relatively higher trophic levels because of the absence of other controlling factors (e.g. predation; Fig. 1a). On the other hand, (2) predation regulates the number of species present in guilds of low trophic status (Fig. 1a). Between communities and between habitats, competition should be relatively more important than predation as an overall organizing factor in communities with few trophic levels (Fig. 1b). Further, because predators seem less capable of dealing with environmental harshness than do their prey (Connell, 1971), such trophically simple communities should occur in physically rigorous environments. In more moderate physical environments, species of higher trophic status can persist and predation should become relatively more important as an overall organizing factor (Fig. 1b).

An important qualification to this model clarifies an apparent contradiction. In some systems with complex trophic organization, the species providing most of the visually obvious community structure are of low trophic status (plants such as trees, kelp, other macroalgae). Further, in many systems plants probably compete for space

A. Within Community



B. Between Community

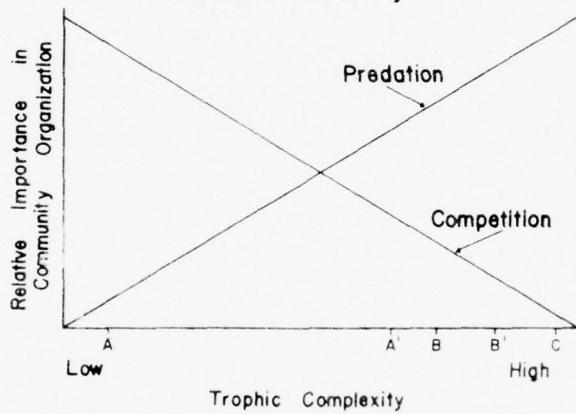


Fig. 1. Qualitative model of the relative within-community (A) and between-community and habitat (B) importance of interspecific competition and predation in organizing communities. The relationships are linear for convenience and are not intended to convey any particular quantitative relationship. Suggested positions of communities discussed in the text are: A - A', New England exposed to protected areas; B - B', Pacific Northwest coast exposed to protected areas. C indicates the region which communities of great trophic complexity are hypothesized to occupy. These might include some coral reef communities, kelp forests in the Pacific Northwest and southern California, the subtidal community in McMurdo Sound, Antarctica, deep-sea communities, etc.

and light under natural conditions. Nonetheless, the diversity of these plants and thus a major part of the observed community structure may still be an increasing function of predation intensity on juvenile stages (e.g. Connell, 1971, Janzen, 1970). That is, the adult plants in these systems may represent those that have "escaped" predators (and other sources of mortality) (Connell, 1975b). Experimental evidence from all the systems mentioned above supports this interpretation (Connell, 1971; Dayton, 1975a,b; J. Menge, 1975).

Predictions of the Model

Three key predictions of this model are that, along gradients of decreasing environmental rigor, (1) predation should be increasingly important in organizing communities, (2) predator effectiveness should increase, and (3) within any particular community, the number of species coexisting in the top trophic level should be primarily a function of competition. Removal of a competitor should result in some sort of niche expansion by the remaining competitors.

Prediction 1. Predation should be increasingly important in organizing communities along gradients of decreasing environmental rigor.

I have tested this hypothesis at areas located along a gradient of exposure to increasing wave shock in New England (B. Menge, 1976; B. Menge and Sutherland, 1975), an example of which is given in Fig. 2. This figure (1) summarizes major features of community structure at typical exposed and protected rocky mid intertidal areas in New England, and (2) gives typical results of predator exclusion experiments at such areas. Clearly, predation by the gastropod *Thais lapillus* has no influence at exposed areas while at protected areas it is the factor preventing the dominant competitor for space, the mussel *Mytilus edulis*, from monopolizing primary space (Fig. 2). Moreover, when predators are excluded, only two species co-occur in the mid intertidal at protected areas (excluding ephemeral algae), while approximately eight species co-occur in the presence of the competitor (Fig. 2). A comparable predation effect along a gradient of exposure to waves has been documented on pilings on the coast of New Jersey by Peterson (1975a, personal communication). Combining these studies with earlier ones (Dayton, 1971, Hall, *et al.*, 1970; Paine, 1966, 1971, 1974), the maintenance of high species richness by predation has been experimentally demonstrated in at least five distinct habitats. Moreover, these studies (at least

COMMUNITY ORGANIZATION OF
NEW ENGLAND ROCKY INTERTIDAL

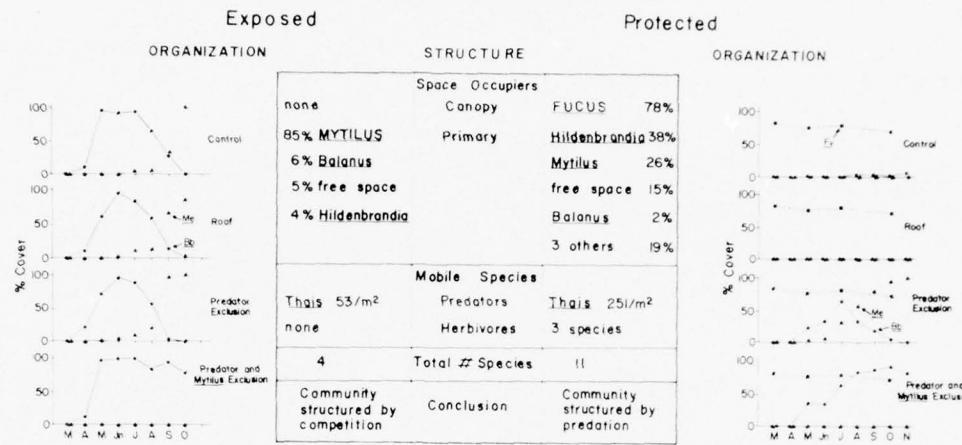


Fig. 2. A summary of the structure and organization of exposed and protected mid intertidal communities in New England (from B. Menge 1976). Abundance of space occupiers is mean percent cover of primary or canopy space. Though present at exposed areas, *Thais* have no effect on community structure (see Table 2). The predator exclusion experiments are examples taken from B. Menge (1976). The predator and *Mytilus* exclusion treatment tests the hypothesis that *Mytilus* outcompetes *Balanus* for space when predators are absent. Canopy cover in the protected experiment is the mean cover obtained over the same time interval in transects used to monitor persistence stability of the community (Table 3). Bb = *Balanus balanoides*, Me = *Mytilus edulis*, Fv = *Fucus vesiculosus*. *Hildenbrandia* is an encrusting red alga.

the marine ones) have been done in physical environments with quite different levels of environmental variation, stress, and predictability. The studies on the east coast of North America, which subjectively seems a less physically stable environment (e.g. B. Menge and Sutherland, 1975, Sanders, 1968) showed that the intensity of predation and competition were inversely related to each other with predation intensity increasing with increasing physical environmental stability (e.g. B. Menge, 1976; B. Menge and Sutherland, 1975; Peterson, 1975). On the more physically stable west coast, predation is the main structuring agent; competition for space occurs only when predators are excluded regardless of relative physical stability (Dayton, 1971; Paine, 1966, 1974). Hence, as predicted, the effect of predation on community structure (distribution and abundance, species richness) increases with a decrease in environmental rigor.

Prediction 2. Individual predator effectiveness should increase along gradients of decreasing environmental rigor.

This prediction is actually a statement of the mechanism of Prediction 1 and has been suggested before (Connell, 1975b, B. Menge, 1976; B. Menge and Sutherland, 1975). In New England, *Thais* is functionally the only mid intertidal predator at most areas (B. Menge, 1976). This gastropod preys primarily on *Mytilus* and *Balanus* (B. Menge, 1976; Fig. 2), two species providing much of the spatial structure of the rocky intertidal community (Fig. 2). To test the hypothesis that per individual *Thais* effectiveness increases with decreasing exposure to waves and decreasing desiccation, I ran a series of field experiments (to be more fully published elsewhere) designed to provide an "index" of *Thais* effectiveness under different conditions (e.g. exposed vs. protected, desiccated vs. moist habitats, etc.). Briefly, these experiments yielded data on the number of mussels (out of twenty per cage per experiment) eaten by five *Thais* in a cage placed in the mid intertidal at an exposed point and a protected cove. At each area cages were placed in the high and low mid intertidal region, under algal canopy or not, near and away from crevices, etc. There were four replicates per treatment and each experiment ran from three to seven days. Size of mussels and *Thais* were kept the same through all experiments. Some results are given in Table 2. In the lower mid intertidal (first, second, and fourth columns in Table 2), high levels of wave shock reduce the number of mussels eaten by *Thais*, although the difference is not significant in one of the three cases. Note, however, that the number of mussels eaten in

Table 2. Predator effectiveness under different environmental conditions.

Exposure to Wave Shock	Relative Desiccation Intensity ^a				
	High (No canopy)	Low (canopy)	High (High inter- tidal)	Low (Low inter- tidal)	
Exposed	36	145	75	128	
Protected	65	161	43	183	
χ^2 (Exposed to Protected) ^b	8.33**	0.48	8.68**	9.73**	
χ^2 (2 x 2)		4.24**		17.22**	

^aNumber in each cell is the number of mussels eaten summed over several experiments (9 or 6) and four cages per experiment. The first two columns are summed over nine low-mid intertidal experiments. The last two columns are summed over six high-mid low-mid intertidal experiments.

^b * = significant at the 5% level; ** = significant at the 1% level.

high intertidal cages was greater (rather than less) at the exposed area than at the protected area. This suggests that severe desiccation is sometimes more inhibitory to *Thais* than wave shock, particularly during summer when these experiments were run. Relatively severe desiccation also reduces the number of mussels eaten when the snails are not under a canopy or are in the high intertidal (Table 2). These results suggest that the effectiveness of *Thais* as a predator is a function of both wave shock and desiccation stress. More generally, these data support the hypothesis that a predator's effectiveness is strongly influenced by its physical environment.

Prediction 3. The number of species coexisting in the top trophic level should be mediated primarily by competition.

This prediction and various related ones have been a focal point of a prodigious amount of ecological research (e.g. MacArthur, 1972; Schoener, 1974). Unfortunately, relatively little of this research has been of an experimental nature (see Connell, 1975a,b, for references). However, in the rocky intertidal, several experimental studies indicate that competition organizes guilds at the top trophic position in a community. At those areas in New England (mid intertidal), in the British Isles and southern California (high intertidal) where predators are naturally absent (or ineffective), the "top" trophic level consists of filter feeding barnacles and mussels which have been experimentally demonstrated to compete for space (Connell, 1961a; Harger, 1970; B. Menge, 1976; B. Menge and Sutherland, 1976). In more trophically complex west coast rocky intertidal communities, competition has been shown to occur between two top asteroid carnivores (B. Menge, 1972b; J. Menge and B. Menge, 1974) and may occur between several species of predaceous gastropods as well (Connell, 1970). Further, when one asteroid (*Pisaster*) is absent from a habitat, the niche of the second (*Leptasterias*) expands, more prey species and larger prey individuals are included in the diet, and its effect on community structure seems to increase (Menge, 1972a,b). In central California, Haven (1973) has indicated that two high intertidal limpets (*Acmaea* spp.) compete for food. Presumably these herbivores occupy the "top" trophic level since invertebrate predators at least are largely absent from the high intertidal at this area. These experiments indicate that competition between these trophically high species is a chronic event and that removal of a competitor tends to result in an expansion of the remaining competitor's niche. However, a thorough test of this hypothesis should also include the experimental

addition of competitors. Ideally, the fate of such an addition would reveal whether or not the number of species in a guild is regulated by competition or some other factor. Unfortunately, such experiments are difficult to perform; further, a failure of an introduced species to persist may be due to factors other than competition (Kohn, 1971; J. Menge and B. Menge, 1974), and truly critical tests of this hypothesis may not be possible.

To summarize, the evidence available supports the model. As suggested by Fig. 1a, the organization of guilds occupying "top" trophic positions in a community, whether they are primary producers, suspension-feeders, herbivores, or carnivores, is strongly influenced by competition. The organization of guilds occupying "low" trophic positions [e.g. the herbivores and suspension feeders preyed upon by *Pisaster* and *Leptasterias* on the west coast of North America (Dayton, 1971; B. Menge, 1972b; Paine, 1974) or by the starfish *Stichaster* in Australia (Paine, 1971)] is determined by predation. Further, as suggested by Fig. 1b, overall community structure is a function of competition when communities are trophically simple (e.g. exposed communities on the east coast) and of predation when communities are trophically complex (e.g. most west coast communities). To illustrate these points more clearly and to suggest extension of them to other less well-known systems, I have indicated regions on the model along which various systems may hypothetically occur (Fig. 1b). I should emphasize, however, that a key feature of the model is the trophic complexity of the community. Thus, trophically simple tropical systems such as the "cryptic" communities studied by Jackson and Buss (1975), may well occur toward the left end of Fig. 1b while trophically complex polar systems like the subtidal sponge-dominated communities in the Antarctic (Dayton, et al., 1974) may occur toward the right end of Fig. 1b.

PERSISTENCE AND ADJUSTMENT STABILITY IN THE ROCKY INTERTIDAL

The understanding of community stability in different habitats has been traditionally hampered by (1) semantic confusion over the meanings of the term "stability", and (2) a lack of good quantitative information on the phenomenon itself. Ecologists have recently begun to grapple with both of these problems, with the immediate result that the problem seems more confused than ever. Nonetheless, some important advances in our understanding of stability have been made. Several authors have suggested that community stability be recognized to have two components:

persistence stability (= persistence = stability) and adjustment stability (= resilience = elasticity) (Holling, 1973, Margalef, 1969; May, 1973). Persistence is generally held to be the degree to which a system varies around some sort of mean value over time, while adjustment stability is generally viewed to be the relative ability of a disturbed community to return to some pre-disturbance state (Margalef, 1969). This usage is gaining increased popularity among field workers (e.g. Hurd and Wolf, 1975; Peterson, 1975b; Sutherland, 1974) and will be followed here.

A major global pattern of apparent community behavior which led to the near-enshrinement of the idea that community diversity or complexity begets stability is that tropical communities are more stable (persistent) than temperate ones (e.g. Elton, 1958). This idea has always been viewed with skepticism by some ecologists and the theory behind it has recently been examined in devastating detail by May (1973). A current view of global variations in community behavior is that tropical communities seem to possess more persistence (i.e. to change little in "appearance" or relative abundance of most species) but less adjustment stability than do temperate or polar communities (e.g. Frank, 1968; Futuyma, 1973; Holling, 1973). To use Lewontin's (1969) terminology, tropical systems possess more local or neighborhood stability but less global stability than do temperate or polar systems.

To test these hypotheses, one must (1) measure the persistence stability of systems in localities differing in stability of the physical environment, and (2) determine the adjustment stabilities of these systems by subjecting them to perturbation analysis. In some ways it is amazing that neither of these problems has attracted much attention until very recently (e.g. Hurd, *et al.*, 1971; Hurd and Wolf, 1975; Peterson, 1975b; Sutherland, 1974).

Persistence Stability in the New England Rocky Intertidal

Jane Menge and I have been studying persistence and adjustment stability at areas of different wave exposure in the New England rocky intertidal for up to four years at some areas. To measure persistence stability, we have run transects, described more fully elsewhere (J. Menge, 1975; B. Menge, 1976), at three intertidal levels (high, mid, and low intertidal), at several areas. These transects yield estimates of percent cover of all space occupying species and of abundances of all mobile species. From these data, relative abundances, species richness, and other aspects of community structure can be estimated. Early in our work we subjectively judged the physical

environment at exposed headlands to be more rigorous, particularly with regard to wave shock, than rocky areas in coves and other leeward areas. This pattern has been quantified and confirmed using the loss rate of experimental cages at all areas (B. Menge, 1976).

Table 3 shows several preliminary measures of persistence stability (average percent change/month in percent cover, average monthly variance in percent cover, average variance/mean percent cover) at an exposed area, a protected area and an area of intermediate exposure. In general, the exposed area has the least persistence stability, though the correlation is not perfect. For example, average monthly variance is greater at the intermediate area than at the exposed areas (Table 3). Further, the intermediate and protected areas are very similar when mean change per month in percent cover is compared. Subjectively, the difference in persistence stability is strongly correlated to wave exposure. That this correlation is not so clearly apparent in the data is probably due to very severe storms preventing us from sampling some areas, especially the exposed one, at strictly regular two-month intervals. Of the measures in Table 3, probably the best are those based on the variance/mean ratio since mean abundance of the most common species can vary so widely at any particular time. Note particularly that the mean/variance ratio of the dominant (in terms of biomass) species is most unstable at the exposed area (*Mytilus* at Pemaquid Point, $s^2/\bar{x} = 13$), is intermediate at the intermediate area (*Fucus vesiculosus* at Grindstone Neck, $s^2/\bar{x} = 6.6$) and is least unstable at the protected area (*Ascophyllum nodosum* at Canoe Beach Cove, $s^2/\bar{x} = 3.5$). Since these species are among the most visible features of community structure, the close correlation between their persistence stability and wave exposure probably accounts for the strong subjective correlation between persistence and physical stability noted above.

In general then, the most stable (persistent) communities seem to occur in the most stable environments. Note, however, that persistence stability at the population level is sometimes uncorrelated with physical stability (e.g. *Mytilus*, s^2/\bar{x} , Table 3). This pattern has been noted in other systems (e.g. Peterson, 1975b) and suggests that a clear understanding of basic global patterns of persistence stability awaits further study.

Adjustment Stability in the New England Rocky Intertidal

Adjustment stability in New England rocky intertidal communities is being studied by examining the rate of

Table 3. Measures of persistence stability in New England rocky intertidal communities.

Measure	Level of Biological Organization	Area		
		Pemaquid Point (exposed)	Grindstone Neck (intermediate)	Canoe Beach Cove (protected)
Mean change per month in mean percent cover	Community Population	3.9±1.6	2.2±1.0	2.3±0.3
	<i>Balanus</i>	4.3±2.1	0.3±0.1	1.5±0.4
	<i>Mytilus</i>	4.8±1.2	2.6±0.6	2.1±0.6
	fucoid	1.0±0.3	2.5±0.6	2.7±0.6
	free space	5.3±2.0	4.5±1.4	4.1±0.9
Mean monthly variance (n = 10 quadrats/month)	Community Population	346.1	415.2	193.3
	<i>Balanus</i>	351.9	1.4	15.9
	<i>Mytilus</i>	662.8	581.9	185.0
	fucoid	66.4	530.2	294.7
	free space	303.1	547.1	277.7
Mean variance/mean (s^2/\bar{x})	Community Population	15.3	9.9	8.4
	<i>Balanus</i>	13.4	1.0	3.8
	<i>Mytilus</i>	13.0	22.1	23.8
	fucoid	11.5	6.6	3.5
	free space	23.5	9.7	3.6

return of a community to the pre-disturbed state. The disturbance consisted of removal of the sessile species dominating mid intertidal spatial structure at the exposed, intermediate, and protected areas (dominants are *Mytilus*, *Fucus vesiculosus*, and *Ascophyllum nodosum*, respectively) with a putty knife. The perturbations were performed in March, 1974, and they and their controls were subsequently monitored as often as possible. Abundance of all sessile and mobile species was estimated from transects or photographs of the treatment (see caption of Fig. 3 for details). These perturbations mimic the effects of natural disturbances relatively closely in both their timing (most physical disturbance is in winter and early spring) and effect.

Compared to Table 3, Fig. 3 indicates that if resilience is measured by how rapidly the spatial dominant is reestablished, the least persistent community (exposed) has the greatest adjustment stability and the most persistent community (protected) has the least adjustment stability. At the exposed area, removal of *Mytilus* in March is succeeded by dense settlement of *Balanus* in April and May; these barnacles are subsequently settled upon by *Mytilus* and outcompeted by September-October. Thus, the original configuration is reestablished within seven months (Fig. 3). (However, this return rate is dependent on the time of disturbance. Other experiments not presented here have shown that if the disturbance occurs after *Balanus* settlement, mussels fail to settle and the community does not rebound for at least eight months and probably will take about nineteen months.)

At the intermediate area, removal of *Fucus* is followed by reattainment of the original configuration within twelve months. This relatively rapid return to 100% cover by this large alga (up to approximately one m long) is achieved asexually, since nearly all the *Fucus* in the experiment regrew (or perenniated) from a small amount of holdfast not originally removed from the rock (Fig. 3).

At the protected area, removal of *Ascophyllum* is followed by an immediate increase in *Balanus* abundance and a slow increase in *Fucus vesiculosus* abundance. As yet, (after twenty months), *Ascophyllum* has not returned to its former dominance, although newly settled individuals are becoming increasingly common (Fig. 3). In this experiment, the appearance of *Fucus* depended on sexual, rather than asexual processes, since little or no *Fucus* was initially present.

These results are substantially more complicated than the relatively simple picture conveyed by Fig. 3. The time of year in which the initial perturbation is made affects the length of time for the system to return to its previous state (discussed above for the exposed area). In addition,

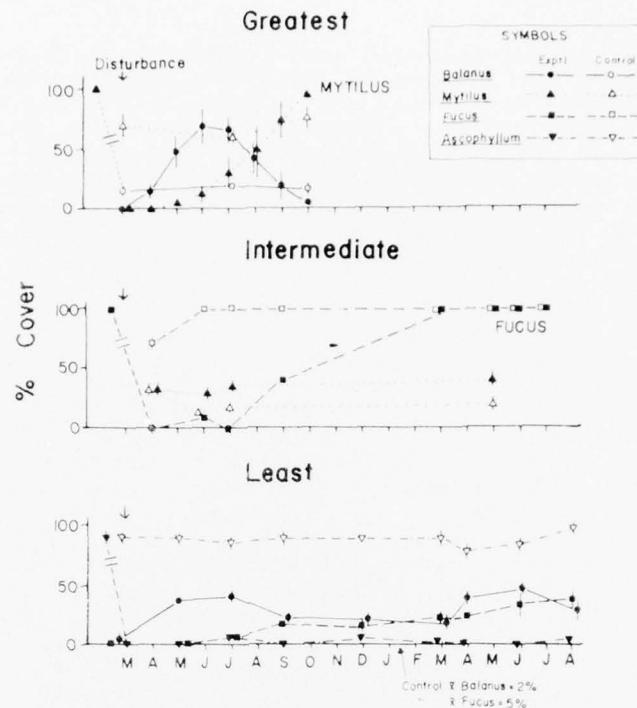


Fig. 3. Preliminary results of perturbation experiments begun in 1974 showing the resilience of areas of great, intermediate, and low exposure to wave shock. Only the abundances (\pm one standard error; percent cover transformed by the arcsin transformation) of the most abundant structural species is plotted. Data at the exposed area are taken from controls (area of each = 100 cm^2) of experiments reported earlier (B. Menge 1976). Identical results have been obtained in larger ($1/2\text{ m}^2$ clearances in 1975). The other experiments have not been reported before and are means of $1/4\text{ m}^2$ subsamples of clearances ranging in total area from one m^2 to 18 m^2 . The time of initial perturbations are marked by the arrows with the change in abundances from the disturbance shown by the interrupted lines. Abundance of *Balanus* and *Fucus* in the control at the least exposed area was always low (means below graph) and were not plotted to reduce confusion. At the exposed area, *Mytilus* reaches structural dominance within seven months. At the intermediate area *Fucus vesiculosus* reaches structural dominance within one year. At the protected area, structural dominance has not been reached; *Ascophyllum* is still very scarce and canopy cover by *Fucus* is less than 50%.

other events have influenced these results. A prominent one was the failure of *Balanus* to settle at the intermediate area (Grindstone Neck, Fig. 3). Although this may have some influence on the rate of recovery, the probable effect will be to increase rather than to decrease the return of *Fucus*. Jane Menge (1975) has found that fucoid algae settlement and survival are enhanced by a substratum of *Balanus* because the microspatial heterogeneity of a dense patch of barnacles provides a refuge for these algae from herbivores (periwinkles). Thus, *Fucus* abundance at this area would be supplemented by settlement and growth of barnacles coupled with a relatively small population of periwinkles.

In contrast, periwinkles are very dense at the protected area (unpublished data). If herbivores are excluded, *Fucus* will occupy 100% of the canopy space within six months (J. Menge, 1975). Hence the rate of increase in *Fucus*, and perhaps *Ascophyllum*, abundance at the protected area is undoubtedly slowed by herbivory. Thus, herbivores have a major influence on apparent community resilience.

At all intermediate and protected areas examined (B. Menge, 1976), predator exclusion usually results in rapid monopolization of space by *Mytilus* (e.g. Fig. 2, exposed results in Fig. 3). Once *Mytilus* occupies most primary space, survival of adult *Fucus* declines and settlement of both fucoids rarely occurs, since *Mytilus* both outcompetes already established *Fucus* (at least) (J. Menge, 1975, B. Menge, 1976) and probably also filters their gametes from the water column, preventing recruitment (Dayton, 1973; J. Menge, 1975). Thus the global stability characteristics of a system can result from a complex of biological and physical factors.

These experiments on adjustment stability tend to support the belief that communities in relatively benign habitats are more persistent, but less resilient than are communities in relatively rigorous habitats. If this is generally true, then the next step is to learn what factors account for such differences in community dynamics. The above results, with the following outlines of life histories of key component species, suggest that community stability is a function of (1) the particular mix of life history strategies possessed by the structurally and functionally dominant species, and (2) the relative intensity of biological interactions, especially consumer-prey interactions.

Life Histories, Biological Interactions, and Community Stability

In the New England systems considered above, the structurally dominant species are increasingly longeuous.

Summarizing unpublished data and observations, *Mytilus*, *Balanus*, and a large proportion of other species commonly occurring at exposed areas (e.g. ephemeral algae) are relatively short-lived and evidently can mature within two years and perhaps as quickly as one year. Settlement success of these species is usually high. Thus, exposed, *Mytilus*-dominated communities are characterized by a high degree of opportunism.

At intermediate areas, *Fucus vesiculosus* thalli seem to persist for periods on the order of five to ten years (*Fucus* has great perennation abilities and may actually be near-immortal). Recruitment of *Fucus vesiculosus* occurs continuously from spring through autumn (J. Menge 1975, personal observations). On the average, this species seems longer-lived than *Mytilus*.

At protected areas, *Ascophyllum* is apparently very long-lived, perhaps up to fifteen years (Vadas, personal communication, personal observations). This alga has poor recruitment success, even when herbivores are excluded. Finally, its perennation abilities appear far inferior to those of *Fucus vesiculosus*. Hence the relative degree of opportunism of the structurally dominant species declines and their longevity increases with a decline in environmental rigor. Subjectively, relatively many species characteristic of *Ascophyllum*-dominated communities appear more longevous than species in more rigorous New England intertidal communities.

The idea that life histories have a major effect on the apparent resilience properties of a community is supported by current reinterpretations of succession theory (Connell, 1972; Drury and Nisbet, 1973; Horn, 1974; Keever, 1950). These authors consider that secondary succession, which might be defined as the collection of processes occurring when a community is rebounding or redeveloping from a disturbance ("resilience processes"), is more influenced by life histories of the component species than by habitat alteration and a rigid, serial replacement of species. Basically the successional sequence is viewed to be determined by different dispersal, settlement, growth and competitive abilities of the species in the sequence. An early species may be early because it is more opportunistic than a late one and not because a late one cannot tolerate the physical environment in the initial stages of succession. The actual replacement of a species by another is suggested to be regulated in part by interspecific competition. In addition, my experiments and those of J. Menge (1975) suggest that consumer-prey interactions can be exceedingly important in determining (1) the rate of return to the predisturbance state, and (2) the state the system returns to after disturbance. Thus, in the absence of

predators a totally different state is reached (e.g. Figs. 2, 3). The presence of predators may also influence the recruitment success of fucoids by preying on the barnacles and changing the availability of micro-refugia (J. Menge 1975, see above). Further, herbivores probably slow the return to a pre-disturbance state by preying on the young of the structural dominants (J. Menge, 1975; see above). To summarize, decreasing community resilience with increasing environmental stability may be a function of (1) life history differences of major component species, (2) competitive interactions, and (3) increasingly intense effects of consumers on their prey. Hence, the fragility of these systems may well be a function of their organizational complexity (e.g. Horn, 1974, May, 1973).

DISCUSSION

One of the delights of nature is its endless variety; an equally satisfying and delightful feature is the apparent arrangement of this variety into clusters of recognizable, repeated patterns. The task of ecologists and evolutionists is to determine whether or not the mechanisms behind this repetition also fall into recognizable, repeated patterns. A particularly critical problem is to determine how widely operational are organizational mechanisms such as those discussed in this paper. I feel the results obtained in rocky intertidal systems have a much broader application than many ecologists suspect. This opinion is clearly and reassuringly shared by others (e.g. Connell, 1975b; Dayton, 1975; Hall, *et al.*, 1970; Paine, 1974). Nonetheless much more community-oriented, experimentally-based field research in a variety of terrestrial and aquatic habitats in environments of varying rigor is necessary to resolve the issue. A particularly relevant, very recent result is that in certain tropical marine subtidal communities, the organizational effects of competition seem to operate in a somewhat different manner (Jackson and Buss, 1975) than in temperate intertidal systems. These workers suggest that the observed high diversity in cryptic communities (which are rarely affected by predation) is a result of competitive "networks" (A outcompetes B which outcompetes C, but C outcompetes A) rather than the better known competitive hierarchies (A outcompetes B and C, B outcompetes C, C outcompetes no one) found in intertidal systems. In other words, competitive exclusions are much less likely to lead to monopolization by a single species in these cryptic communities than in intertidal communities.

It thus appears that much understanding of broad

patterns of community structure and behavior can be achieved by an experimentally based understanding of both the short-term and long-term consequences of interactions between species. Patterns of community structure (e.g. species diversity, distributional patterns, relative abundances, and productivity) and community behavior (e.g. resilience, persistence) are all greatly affected by predator-prey and competitive interactions acting within the constraints applied by characteristics of the physical environment.

Acknowledgements

I thank M. Rex and J. Menge for providing constructive criticism on the manuscript. Field assistance and collaboration has been provided by numerous people; chief among these are S. Garrity, C. Hibbard, and students in the Population Biology class at the University of Massachusetts. Research support was provided by NSF grants numbers GA 35617 and DES72-01578 A01.

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FOULING ON ARTIFICIAL SUBSTRATES
AS A MEANS OF INCREASING THE PRODUCTIVITY
OF NATURAL MARINE ECOSYSTEMS

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Careful inquiry into the question of artificial augmentation of productivity in natural marine ecosystems appears to be one of the most vital theoretical and practical problems of modern hydrobiological research. The intensification of the fishery of economically valuable species, ordinarily playing the leading role in ecosystems, has resulted in a frequently most disastrous and alarming decrease in the number of local populations, causing in turn, a disturbance in the energetic balance within the ecosystems and occasionally even a complete extinction of useful species under certain conditions.

It is manifest that scientific regulation of fishery and certain protective measures cannot alone satisfy the growing necessities of the world population. Therefore, an organization of the mariculture of valuable species, helping to increase the productivity of pragmatically important ecosystems, seems to be a possible solution for the problem.

Numerous research works on the primary production of the sea testify to the fact that in many regions of the World Ocean, a quantity of organic substance is produced, which is sufficient to guarantee abundant development of heterotrophic organisms. The greater part of organic substance is being produced in the upper region of the shelf at the depth of 20-30 meters, where approximately 90% of the whole macrobenthic mass on the shelf is being formed (Golikov, Averintzev, Scarlato, 1974; and others). Ecosystems of temperate waters play a most important part in the bioenergetic structure of the World Ocean. The leading place in the majority of these ecosystems is occupied by bioms of macrophytes, which through their abundance (100 kg/m^2 in certain areas) and through their rapid rate of production can cover the deficiency in primary production both in the low-lying aphotic zones and in the high arctic and antarctic

waters. Also contributing to this are the maximal proficiency and long duration of the development of phytoplankton in the neretic zones of temperate waters. Macrophytes appear to be the most important source supplying the organic substance in the sea (Petersen, Boysen-Jensen, 1911; Mann, 1972; and others). Only a small part of the enormously large biomass, consisting of algae and sea grass, is utilized by local phytophages, while its greater part becomes disintegrated, dissolved, transformed into suspensions and carried away by seastreams to form trophic chains of organisms in remote regions. Furthermore, in mobile neretic waters of temperate latitudes, a sufficient quantity of biogenetic elements can, as a rule, be found. All of these factors favor a most luxurious development of plankton in waters covering the shelf at the period of vegetation and offer a wealth of food for plankton larvae of benthic animals. Accordingly, on the grounds of literary data and our personal investigations (Golikov, Scarlato, 1969), it can be conjectured that the food factor does not limit the number of trade organisms at the plankton phase of ontogenesis. The spawning period of the majority of trade species occurs simultaneously with the extensive development of phytoplankton and the appearance of a sufficient amount of small plankton animals.

The number of planktonophagous predators in neretic waters is small, compared to the great number of larvae of benthic animals. Therefore, in many neretic regions the presence of predators also does not limit the quantity of meroplankton.

The lack of suitable substrates for the settling of young under other favorable conditions appears to be a more important factor, actually limiting the quantitative development of species with a plankton phase in ontogenesis. Larvae of many benthic species, including trade species, in the early post-larval stages of ontogenesis, need a quite definite substrate for their settling and successful development.

Thus, for example, larvae of food molluscs *Mytilus edulis*, *Patinopecten yessoensis*, and others, settle on the algal foliage and on the leaves of the sea grass (a thread-like substrate), and oyster larvae on a hard substrate of light color, etc. Substrates of this type form a narrow line along the coastal region alone. In addition, the successful progress of larval metamorphosis may be impeded by other physico-chemical factors or by inappropriate biotic surroundings, even if there are considerable areas with suitable substrates. Due to both of these facts, a large mass of larvae may slow down its metamorphosis and perish, even if it has succeeded under unfavorable conditions.

Under conditions favorable for the settling and

development of the young in small districts, surrounded by large areas of unfavorable physico-chemical environment, there can be observed an augmented abundance of life. This phenomenon, known in science as the "refuge-effect," calls forth an enormous concentration of life in the coral reefs, surrounded by vast areas of oligotrophic tropic waters (Golikov *et al.*, 1973).

The presence on the shelf of adult individuals belonging to the same species has proven to be an important factor, stimulating the settling of the larvae of the species which then form aggregations.

The positive chemotaxis of larvae to substances secreted by adult specimens of the same species (Allee, 1931; and others) is most important in some cases, while in other cases, the chromo-orientation of larvae to the background, coinciding in color with parental individuals, is of greater importance (Thorson, 1964; and others).

The number of young which have started the imaginal phase of life in natural ecosystems is considerably reduced by predators. Thus, the young of the food - bivalve molluscs - which have begun their bottom life, thanks to their small size and relative defenselessness, are devoured in great numbers by the benthos-feeding predators, particularly by starfish.

The "refuge-effect," caused by arranging artificial substrates in districts with other favorable physico-chemical conditions for the settling and development of the young, together with measures directed toward the protection of the growing young from predators, may create conditions favorable for a considerable increase in productivity of marine fishery regions. Thus, study of the process of formation of epibioses on natural or artificial substrates has essential pragmatic significance, as well as theoretical interest for knowledge of the regularities of biological successions.

To study the above problem we have undertaken a series of experiments in the Possjet Bay, Sea of Japan; we arranged artificial substrates to learn both the process of succession development in these waters and the settling and growth conditions of the young belonging to fishery species.

Collectors - anchored rafts with substitutes of natural substrates suspended from them (cotton and capron nets, sizal and jute ropes, bunches of birch bezoms, shells of *Patinopecten yessoensis* and *Crenomytilus grayanus* strung on a cord) - were placed during May, 1965, in half-protected bays and in relatively open parts of the Possjet Bay.

We continued our observations until the next summer; they are now being conducted by the scientific workers of the Pacific Institute of Fishery and Oceanography and of the Institute of Marine Biology of the Academy of Sciences of

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the USSR in Vladivostok. As we have learned from our observations, fouling on artificial substrates began almost immediately when they were placed underwater. At first, a bacterial pellicle developed on the substrates, then flocks of detritus began to appear. The substrates were then populated by numerous infusoria and later by populations of bottom Diatomea of extraordinary density. In the beginning of June, organisms of meiofauna pervaded the collectors and algal growth appeared. Of all the organisms of meiobenthos, Harpacticoida came in greatest quantity, so that the number of their individuals reached the hundreds of thousands per 1 m² of substrate surface toward the middle of June. The organisms of meiobenthos were followed by larvae of macrobenthic organisms, which began to succeed and settle on artificial substrates in large numbers and, due to their rapid growth, soon took the leading place in the growing biocenoses by their biomass. A similar order of development is followed by fouling epibioses on artificial substrates in other regions of the Sea of Japan (Gorin, 1969), in the Mediterranean Sea (Taramelli, Chimenz, 1966; Sentz-Braconnat, 1966; and others), in the Black Sea (Dolgopolskaya, Braiko, 1974; and others), in the Baltic Sea (Arndt, et al., 1974; Scheibel, 1974; and others), in the North Sea (Persoone, 1971; and others), and in Messina Bay (Gorbenko, 1968; and others), etc. It seems therefore, reasonable to assume that the substitution of large taxonomic groups in the process of succession of fouling epibioses on substrates isolated from the ground follows a general rule which is independent of the special peculiarities of environment in each region. Only the dates and rate of successions are noticeably different.

In the northern hemisphere, the rate of development of fouling biocenoses reaches its maximum in late spring, summer, and early autumn, and diminishes abruptly in winter.

In latitudes further north and with lower salinity, the process of succession is slower and less variegated than in southern regions (Meadows, 1969; and others).

In most cases, after a short period of succession, large macrobenthic organisms approach the substrates, depending upon the water (mostly sestonophages and filtrators, more seldom - algae).

The systematic affinity of the dominant species is determined by organisms which play the leading role in the aquatorium. In most regions, the dominant role in the fouling biocenoses is taken either by Spongia (Taramelli, Chimenz, 1966; and others) or by Cirripedia (Turpaeva, 1967; Bagirov, 1968; Long, 1972; Gorin, Murachvery, 1973; and others), Hydrozoa (Kuznetzova, 1967; and others), Algae (Zavodnik, Igit, 1968; and others) or Bivalvia (Kuznetzova, Zevina, 1967) which have won the competition among different

life forms for their place on the substrate.

In our experiments, species of Gastropoda maintained their predominance on collectors of different types. They seized this position soon after the meiofauna had developed and kept it until the end of June; then in the first half of July, the gastropods were followed by species of Bivalvia, which played the leading role in the fouling biocenoses from that time until the end of the experiment. This position of dominant species in our experiments corresponds to the climacteric state of a series of epibioses on natural substrates in the Possjet Bay.

A successive change of the dominant position in growing epibioses of different large phylogenetic groups, determined by the season of the year or by the phase in the development of fouling epibioses, was observed by other authors as well (Kuznetzova, 1967; Gorin, Murachver, 1973; Chimenz, et al., 1974; and others). It is typical that in our experiments the larvae of Gastropoda had the quantitative predominance in the plankton at first, but were then succeeded by Bivalvia.

Considering that the period (temperature) of spawning of each biogeographic group of species is determined, the change in the predominance of large taxonomic groups both in the plankton and in the process of succession of fouling epibioses may be caused either by a stronger development of a certain definite biogeographic group of species in each of the taxons, or by a different time of larval development in the plankton, determined by their morphological peculiarities, or by both of these factors.

In the Possjet Bay, we observed that the spawning of species of different biogeographic and phylogenetic groups took place in the following order. In the last ten days of May, when the water temperature reached $+10-+12^{\circ}\text{C}$, there began a massive spawning of many low boreal species, including such trade species of Bivalvia as *Patinopecten yessoensis*, *Crenomytilus grayanus*, *Modiolus difficilis*, *Spisula sachalinensis*, and others. By that time, larvae of a less warm water species of Gastropoda, *Epheria turrita*, dominated in the meroplankton. Larvae of *Mytilus edulis*, which later became most abundant, were also found in the plankton. In the second half of June, larvae of the above-cited low boreal species of Bivalvia began to dominate in the meroplankton. At the end of June and beginning of July, when the water temperature reached $+18-+19^{\circ}\text{C}$, species subtropic by origin began spawning, including such food organisms as the trepang, *Stichopus japonicus*, and the oyster, *Crassostrea gigas*. At the end of July and in August, larvae of these species began to dominate in the meroplankton.

The change in the number of species with succession in the fouling biocenoses has a regular, undulating, wave-like

character.

In protected and open bays, the succession of changes in the number of species proves to be comparable; but in the former, which are well-warmed in summer, these changes proceed at a greater rate and are more marked (Fig. I A,B). The variability of the number of species on different substrates is also of a wider range in protected bays than in open bays. The greater number of species, both in protected bays (10 species per 1 m² of substrate surface) and in open bays (17 species per 1 m² of substrate surface), settles on the cotton nets. In June, the number of species increases due at first to the growth of meiofauna, and then due to the appearance of the young Polychaeta, Amphipoda and such low boreal species of Gastropoda as *Epheria turrita*, *Homalopoma sangarense*, *Alaba vladivostokensis*, *Setia ornata*, and others. By the beginning of July, in protected bays (and after a week, also in open bays) the number of species on collectors is being reduced due to elimination and migration; in the second half of July, however, the diversity of species again increases due to the settling on the collectors of larvae of a series of Bivalvia, Hydrozoa and Bryozoa from the order of Cheilostomata. At that period of time, at first in protected bays and then approximately two weeks later in less protected open bays, side by side with larvae of *Mytilus edulis* and *Musculista senhousia*, which were still settling, larvae of *Patinopecten yessoensis* settled on the thread-like substrates (nets, ropes). At the beginning of August, larvae of *Crassostrea gigas* settled on the vacant shells of the light-colored background. The next stage in the marked decrease in the number of species of successors occurred by the end of August due partly to a rapid growth of the young of large bivalve molluscs and to the reduction of free areas in the collectors.

In September, as a result of both the autumnal peak in the spawning of a series of species and the settling on the collectors by the young of such warm water species as *Chlamys farreri nippensis*, and due to the fact that the surface of the shells of adult Bivalvia had been used as secondary substrates, there occurred another fresh increase in the number of species. A rapid temperature drop in autumn caused a fresh reduction in the number of species on artificial substrates.

As is obvious from the above data, no stabilization in the number of species within the restricted area of the collectors is observed while succession is in progress, which could have been expected from the MacArthur-Wilson model of the population of small isolated islands. From our point of view, the lack of stabilization results from the extensive variability in environmental conditions in the upper layer of temperate waters, and from the increase of inter-specific

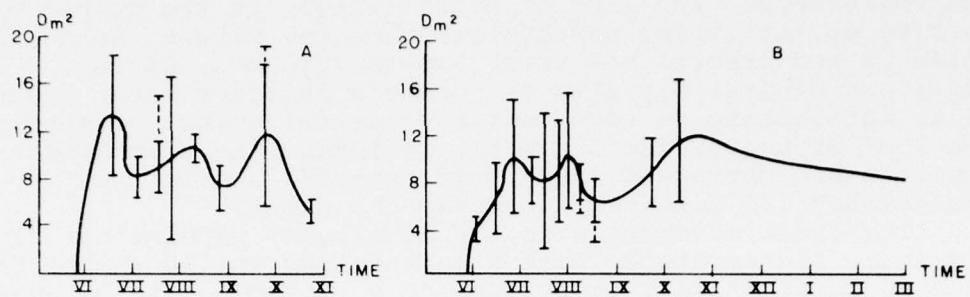


Fig. 1. The change in the number of species on artificial substrates according to the time of their exposition. A - in protected bays, B - in open bays. The ordinate shows the average number of species on 1 m^2 of artificial substrate, and the abscissa shows the time of exposition of the substrates (months). The vertical lines show the variability in the number of species on different types of substrates.

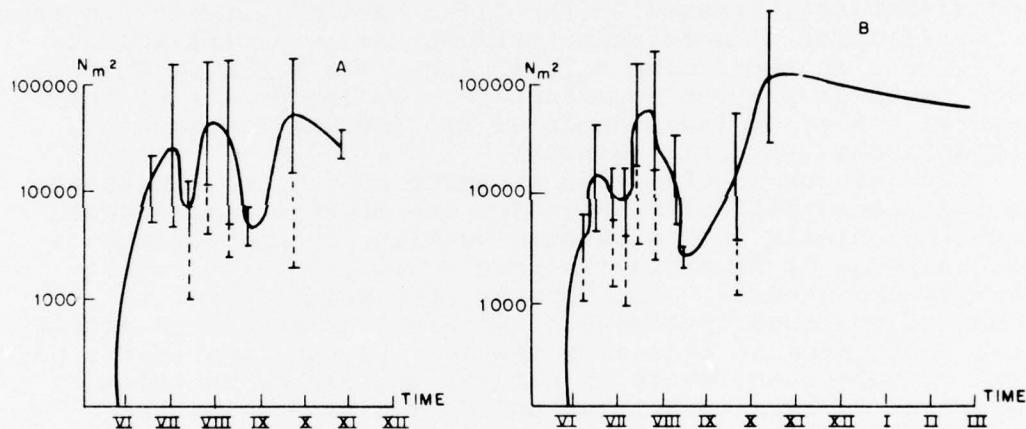


Fig. 2. The change in density of populations of organisms on artificial substrates according to the time of their exposition. A - in protected bays, B - in open bays. The ordinate shows the average density of populations of organisms (N) per 1 m^2 of substrate surface (logarithmic scale), and the abscissa shows the time of exposition of the substrates (months). The vertical lines show the variability in the number of individuals on different types of substrates.

competition for habitation areas on the restricted area of the collectors. The lack of stabilization in the number of species on artificial substrates in marine waters (Schoener, 1974a,b; and others) and fresh waters (Dickson, Carins, 1972; and others) may also be observed in other water bodies. It is interesting to note that the maximal number of species per 1 m² of the surface of artificial substrates in Massachusetts Bay (Driscoll, 1968 - 16 species) and in the Possjet Bay (20 species) is nearly the same.

The order of changes in the density of populations of organisms is comparable to the variability in the number of species on artificial substrates (Fig. 2 A,B). The greatest variability in the number of individuals on different types of substrates (as well as the greatest number of species) can be observed at periods when the general number of organisms is being increased. The maximal density of populations (exceeding 200 thousand specimens per 1 m² of substrate surface) was observed on the surface of vacant shells of *Patinopecten yessoensis* and *Creomystilus grayanus* at the beginning of July and August. The number of organisms in the first stages of succession of the fouling biocenoses (not taking into account a large number of bacteria, infusoria and diatoms) increased in the first half of June due to the multiplication of meiofauna, predominantly Harpacticoida.

Then, in the second half of June, the young of Gastropoda began to play an important part in the growth of the general number of individuals in the fouling biocenoses (predominantly *Epheria turrita*).

The growth in the general number of fouling biocenoses in the second half of July and in the beginning of August resulted chiefly from a massive settling on the collectors of the young of Bivalvia (*Mytilus edulis*, *Musculista senhousia*, and others). The density of populations of the young of the food species *Patinopecten yessoensis* on artificial substrates at this time was 1,000-2,000 individuals per 1 m² of substrate, while in natural ecosystems on filigree layers of *Sargassum pallidum* and *S. miyabei* and on the leaves of *Zostera marina*, the population density of this species amounted to 7-15 specimens per 1 m² (Golikov, Scarlato, 1970).

After intensive elimination of specimens at the end of summer, caused both by the fact that a series of species abandoned the fouling biocenoses (including the young of *Patinopecten yessoensis*, which have begun their bottom mode of life) and by the fact that the number of other species has decreased, the density of populations on the collectors is once more greatly increased. This increase in number is caused by the settling of the young of these species, which are spawning at the end of summer and in autumn, and by the forthcoming of additional ecological niches, due to the

rapid growth of background-forming species of bivalve molluscs, which began to play the part of fouling biocenoses.

The specific diversity in fouling biocenoses, calculated as the ratio of the number of species (D) per density of populations (N) per 1 m² of the surface of the collectors, corresponds to the 3 phases of succession of these biocenoses, reflecting the change in the specific number and general number of individuals with the growing succession (Fig. 3 A,B). Due to the fact that the index of specific diversity is inversely proportional to the density of specific populations, (whether calculated by the Shannon-Weiner method or by a simpler method, such as the ratio of the number of species per number of individuals; the ratio D/N has the same biological value and reflects the same successive changes as the informational index of Shannon-Weiner), the maximal specific diversity can be observed during periods when the general number of organisms is being reduced in the collectors.

It is assumed that the increase in specific diversity testifies to a certain complication in the system, the fact that the system has achieved a relative stability. Indeed, the maximal specific diversity, observed in the first half of June, corresponded to the greatest development of biocenoses, where the gastropods prevailed (predominantly *Epheria turrita*).

The collapse and destruction of these biocenoses, caused by the fact that the leading role in the biomass of the fouling biocenoses was seized by *Bivalvia*, resulted in the reduction of specific diversity. The development of biocenoses with *Patinopecten yessoensis* dominant in some regions and *Musculista senhousia* in others, stimulated the growth of specific diversity, which was then followed by a reduction in the general density of populations and a decrease in biomass of the biocenoses (Fig. 4 A,B). The disturbance of stability in these biocenoses at the end of July and beginning of August, caused by the settling on the collectors of species subtropic in origin, resulted in a fresh reduction in specific diversity, while the general biomass and number of individuals in biocenoses were being augmented.

Toward the end of August, the process of succession of the young to the collectors was being halted; the general number of individuals and the biomass of fouling biocenoses was reduced by migration (for example, migration of the young of *Patinopecten yessoensis*) and elimination of individuals of a series of species; and there seemed to occur a temporary stabilization of the structure of fouling biocenoses with the predominance (by biomass) of *Crassostrea gigas* in some districts and *Mytilus edulis*, Algae, Hydrozoa or Bryozoa in others.

The autumnal peak of spawning of a series of

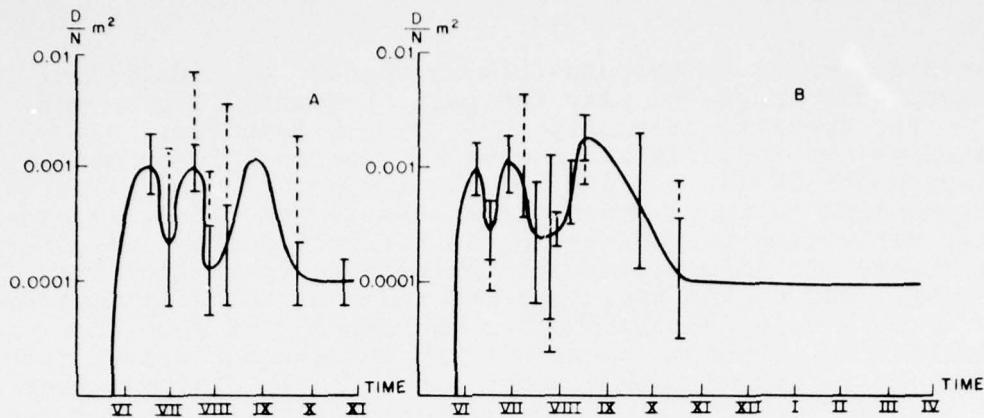


Fig. 3. The change in specific diversity of fouling biocenoses. The ordinate shows the ratio of the number of species per number of individuals (D/N) per 1 m^2 of substrate surface (logarithmic scale), and the abscissa shows the time of the exposition of substrates (months). The vertical lines show the variability in the specific diversity on different types of substrates.

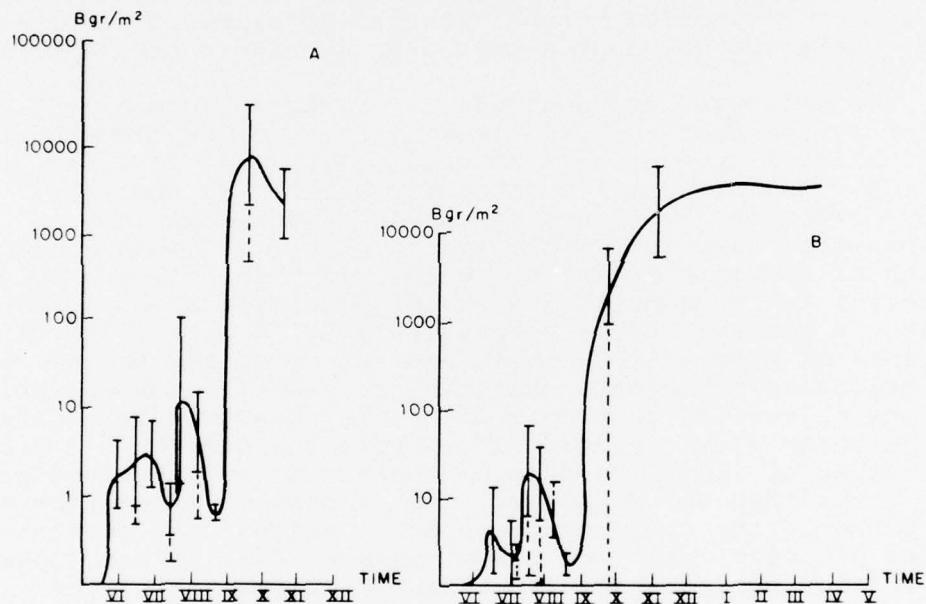


Fig. 4. The change in biomass of biocenoses on artificial substrates according to the time of their exposition. The ordinate shows the average biomass of biocenoses (B) per 1 m^2 of substrate surface (logarithmic scale), and the abscissa shows the time of exposition of substrates (months). The vertical lines show the variability in biomass on different types of substrates.

predominantly widely distributed boreal species and the succession of their young on the collectors, as well as a rapid growth of the young of food bivalve molluscs, caused a new increase in the number of individuals and in the biomass of biocenoses and a decrease of their specific diversity to an experimentally minimum value. A drop in water temperature in autumn (which came more suddenly in protected shallow bays than in deep open bays) caused the cessation of settling of young on the collectors, an abrupt retardation of biological processes and the stabilization of specific diversity at a new reduced level.

The index of specific diversity, estimated by the Shannon-Wiener method, ranged from 0.5 to 2.1 information beats on the collectors, which is evidence of important changes in the number of species and the density of populations of organisms in fouling biocenoses during succession.

The rapid growth of biomass in fouling biocenoses during the last stages of succession is very extensive (Fig. 4 A,B). It is chiefly due to a swift linear and weight growth of food species of Bivalvia, whose individuals grow to an exceedingly large size. Thus, the shell height of young *Patinopecten yessoensis* increased in 3 months so that it became 20-30 mm long; the young of *Mytilus edulis* in 3-4 months toward the cold period grew a shell of similar height, while the shell of the young of *Crassostrea gigas* grew to 60 mm in height in less than 3 months on the collectors; and in 6 months on the collectors there were individuals of the latter species with a shell of 70-100 mm in height and with a well-developed and mature looking muscle. The biomass of *Mytilus edulis* on the suspended bunch of besoms in open bays, more suitable for the rearing of this species, was more than 42 kg per 1 m² of the surface of the fascine, while the young of *Crassostrea gigas* in protected bays, more favorable for the habitation of these species, developed on suspended vacant shells of *Patinopecten yessoensis* a biomass of more than 17 kg per 1 m² of the surface of the shells.

On the ground under natural conditions, the biomass of the young of *Mytilus edulis* did not exceed 270 g/m², while the biomass of the young of *Crassostrea gigas* was 850 g/m². Literary data also offer evidence of the fact that the biomass of sessile organisms in epibioses on suspended substrates grows very rapidly and becomes extremely large (Guliksen, 1971; and others).

On substrates in the water layer in other parts of the Sea of Japan, the biomass of *Mytilus edulis* amounts to 41.5 kg/m² (Gorin, Boykova, 1975), while in the Barents and the White Sea, it reaches 25 kg/m² (Kuznetzova, Zevina, 1967). Near the Kuril Islands, on substrates suspended in the water, biomasses amounting to 22 kg/m² (Rudjakova, 1967) are common,

while in the Caspian Sea the biomass of fouling of *Balanus improvisus* and *Mytilaster lineatus* on artificial substrates is 18 kg/m² (Bagirov, 1968).

Our data, given above, show that the development of life on artificial substrates has a phase-like character.

The change of biocenoses occurs regularly with the growth of successions of the substrates; species of smaller size yield the leading role in biocenoses to organisms of greater size. During the final stages of succession in regions inhabited by epibionthic food species that have a plankton stage in ontogenesis, these species seize the leading role in fouling biocenoses. Excessively large biomasses, created, for example, by food species of bivalve molluscs on artificial substrates, and the ease of their rearing are factors which give full reason to suppose that the introduction of artificial substrates in neretic waters is one of the simplest ways to increase the useful productivity of coastal marine ecosystems.

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RELATIONSHIP BETWEEN LOCAL SPECIES DIVERSITY AND ABUNDANCE
OF HERBIVORES IN THE NEW ENGLAND ROCKY INTERTIDAL COMMUNITY

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The most abundant herbivore in the mid and low littoral zones and in tide pools throughout most of the intertidal region of New England rocky shores is the periwinkle snail *Littorina littorea*. I have experimentally examined the effect this grazer has on algal abundance and diversity in tide pools and on emergent substrata (i.e., rock exposed during low tide) and correlated these results with the herbivore's food preferences as determined in laboratory preference experiments. Field experiments demonstrate that this herbivore controls the abundance and type of algae in high intertidal tide pools. In these pools, the highest species diversity of algae (both H' and number of species) occurs at intermediate *Littorina* densities. This ditonic relationship between algal species diversity and herbivore density occurs because the snail's preferred food (*Enteromorpha*) is competitively dominant to other algae in tide pool habitats. Moderate grazing allows inferior algal species to persist while intense grazing eliminates most individuals and species.

On emergent substrata (in both the mid (fucoid) and the low (*Chondrus* = Irish moss) zones) the herbivore's preferences remain unchanged, but the competitive relationships of the plants are different, presumably because of the different physical environment. On emergent substrata, the preferred plant species are competitively inferior, thus *Littorina*'s grazing decreases algal diversity. On emergent substrata there is a negative linear correlation between algal species diversity (H' or numbers of species) and *Littorina* density.

Thus, this consumer has markedly different effects on algal diversity in tide pools versus on emergent substrata primarily because the relationship between the consumer's preferences and the competitive relationships of the plants are different in the two habitats. These results may typi-

fy the effects of many generalized consumers: when the competitively dominant species is preferred by the consumer there is a ditonic relationship between prey diversity and consumer density; when the competitively inferior species are preferred, there is an inverse correlation between prey diversity and consumer density.

HABITAT STRUCTURE, ABUNDANCE AND INTERACTIONS
OF PREDATORY CORAL REEF GASTROPODS

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The ultimate goal of this research program is to understand the evolutionary processes that have resulted in the very high biotic diversity of tropical coral reefs in contrast to other marine environments. Genera and families with many co-occurring species contribute importantly to this high diversity. The proximate goals of the research are to understand (1) how species with similar environmental requirements use resources in stable, many-species assemblages, and (2) what environmental factors most strongly influence species diversity and abundance.

This presentation will briefly review the first problem and concentrate on the second, with emphasis on the large and conspicuous model genus *Conus*. To determine how similarly co-occurring congeneric species use resources, ecological characteristics of all species are compared in all possible pair combinations. In general, (1) many species pairs do not overlap at all in either food or microhabitat utilization; (2) diets are rarely as similar as microhabitats; (3) species utilizing similar microhabitats have low or no food overlap; (4) species with similar diets have low microhabitat overlap values ($C\lambda = 0.2$); (5) there are some exceptions to the above; (6) at least some of these differences also characterize predatory gastropods similar to *Conus* in size and population density but belonging to the families Muricidae and Mitridae.

The question, what specific attributes of habitats determine species diversity and population density, has been posed in two distinct reef habitat types. In intertidal benches with very low topographic habitat complexity, the presence of refuges from harsh physical conditions, and perhaps from predation, strongly influences population density and species richness of both *Conus* and other predatory gastropods. This has been demonstrated both by correlation analysis and by experimentally increasing habitat complexity

by adding suitable artificial refuges.

Subtidal reef platforms are environments which are topographically more complex, physically more benign, and patchier than intertidal benches. Because many patches are microhabitats unsuitable for predatory gastropods, populations are much less dense, but species diversity is higher. Preliminary analyses indicate that *Conus* population density and species richness are directly related to the proportion of substratum consisting of algal turf binding a thin layer of sand, and inversely related to proportion of living coral cover. Microhabitat selection probably depends both on food availability and avoidance of unsuitable substratum.

The biogenic habitat structure of coral reefs thus profoundly affects the food subwebs in which gastropods are primary carnivores.

MORPHOMETRIC AND ECOLOGICAL DIFFERENCES BETWEEN
GEOGRAPHICALLY SEPARATED POPULATIONS OF THE GASTROPOD
CONUS MILIARIS

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Throughout most of the tropical Indo-West Pacific region the small predatory gastropod *Conus miliaris* occurs commonly in intertidal and shallow subtidal coral reef habitats, which it typically shares with 4-20 congeneric species. However at Easter Island, the most isolated island in the Pacific Ocean, only *C. miliaris* and a recently discovered and evidently rare species represent the genus. Discovery of a habitat supporting only one of a group of similar species that typically co-occur throughout their geographic range provides the opportunity to seek answers to several questions of broad evolutionary and ecological interest:

1) How does the isolated population differ morphologically from more central populations of the same species, and do such differences suggest the geographic origin of the isolate?

Development of a morphometric model of the *Conus* shell has permitted objective analysis of taxonomically important characters. Shells of Easter Island *C. miliaris* differ significantly from those from two eastern Polynesia locations with respect to 7 of 9 characters; the two Polynesia samples do not differ significantly from each other with respect to any. Analysis of shell color by reflectance spectrophotometry also distinguishes Easter Island *C. miliaris* from those from more central Indo-West Pacific localities. Morphometric analyses of radula teeth revealed no significant differences in tooth proportions between Easter Island samples and those from several central localities, but Easter Island specimens have significantly smaller teeth in proportion to shell length than any of the other populations sampled.

2) Has directional selection acting on a small founding population resulted in ecological displacement in response to environmental challenges different from those in the habitat of the source population?

At Easter Island as elsewhere, *C. miliaris* feeds exclusively on polychaete annelids. However, 7 species of polychaetes eaten rarely or not at all by *C. miliaris* elsewhere comprise 79% of its diet at Easter Island. This supports the hypothesis that *C. miliaris* has been ecologically displaced in response to different available resources at Easter Island.

3) Has the isolated population expanded its ecological characteristics in the absence of congeneric potential competitors?

The depth range of *C. miliaris* at Easter Island is greater, and its diet more diverse, than in more central localities where it occurs with several to many congeners, providing evidence for ecological release.

4) Is any such expansion directed toward resources that the absent congeners would be expected to utilize?

Several polychaete species preyed on by *C. miliaris* at Easter Island but not elsewhere are important components of the diets of other *Conus* species in the central Indo-West Pacific region. This indicates that some of the ecological expansion of *C. miliaris* at Easter Island is directed toward resources that absent congeners would be expected to utilize were they present, or if they should colonize the island in the future.

THE APPLICATION OF AN EPIBENTHIC COMMUNITY MODEL

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The epibenthic, fouling community at Beaufort, North Carolina, has been under study since the fall of 1970 to the present time. In conjunction with two field studies, one using settling plates and the other using pilings as artificial substrates, a community model was developed to include certain phenomena which are unique to epibenthic communities of sessile organisms. These are stochastic recruitment processes which result in nonuniform spatial patterns in species abundance. The probabilistic nature of settlement site selection within physically homogeneous habitats is most important for those species with low recruitment rates where only a few larvae will successfully settle. Settlement in these cases is highly conditional upon the availability of the appropriate substrate in sufficient quantities. The actual position of the settlement site, relative to the position of the other species in the community, provides another stochastic feature which can influence community structure. The spatial separation of potential substrate competitors can result in time delays in the expression of competitive dominance as well as complete isolation of these competitors.

During execution of the epibenthic community model, stochastic recruitment, by nine species selected from the Beaufort fouling community, was simulated using relative recruitment rates obtained from field data. Settlement sites within a one-dimensional, spatial array were randomly determined. The recruitment and growth rates were both scaled in time and space. Growth along the spatial array, away from the settlement sites, resulted in competitive encounters. Field overgrowth data were used to determine the structure of a competitive hierarchy. Field observations on intensity and selectivity of predation by sea urchins provided the only source of mortality or species elimination from the spatial array.

Simulated experiments were conducted where intensity and selectivity of the predatory disturbance were varied.

In the absence of any predation, the superior competitors (the sponges, *Halichlona* and *Halichondria*, and the solitary tunicate, *Styela*) were most abundant. As generalized predation intensity increased, *Schizoporella* became most prevalent. This encrusting bryozoan had a high recruitment rate and was often observed in the field to settle quickly and monopolize newly submerged settling plates. When the predation process was modified so as to exclude elimination of the hydroid, *Hydractinia*, high predation intensity selectively favored this species. Field studies have indicated that this hydroid is commonly found on pilings where sea urchins have created sufficient primary substrate for *Hydractinia* settlement. *Hydractinia* had a very low recruitment rate and was very rare on undisturbed substrates. In addition, it was usually found to be not susceptible to sea urchin predation on the artificial piling substrates.

This model has provided additional evidence regarding the mechanisms which favor *Hydractinia* in the Beaufort fouling community. It has demonstrated the interrelationships among predation, competition, and recruitment processes in determining community structure. Current plans are to expand the model to two dimensions and then to apply it to other epibenthic communities. This model is uniquely suited to analyze the relative effects of complex competitive relationships (e.g., networks) and the stochastic recruitment processes which have been reported to be important in certain tropical, reef communities.

MAINTENANCE OF DIVERSITY IN CRYPTIC CORAL REEF COMMUNITIES

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Most of the hard substrate surface area of coral reefs lies within crevices and other cavities of the reef framework. The most common of these cryptic substrates on Caribbean fore-reef slopes are the exposed skeletal undersurfaces of foliaceous corals such as *Agaricia*, *Montastrea*, *Mycetophyllum*, and some *Porites*. These substrates support a highly diverse encrusting fauna of some 300-500 species. Sponges, ectoprocts, colonial ascidians, and coralline algae occupy the largest proportion of the available substrate. Free space is almost entirely lacking (maximum 1-5%) and direct competitive interactions for space (interference competition) are intense. Virtually every coral undersurface exhibits numerous examples of overgrowth of some species by others.

Experimental studies on the rocky intertidal shore have demonstrated that, in the absence of disturbance, substrates become dominated by one or a few species. Higher diversity results from the introduction of a disturbance, either in the form of predation or physical processes, which makes free space available for inferior competitors. This model for maintenance of a given level of diversity is dependent on a ranked hierarchy of interference competitive ability (Species A > Species B > Species C and Species A > Species C) coupled with the maximum effects of disturbance operating upon the competitively dominant Species A.

In the cryptic reef system no obvious disturbance agent is apparent, yet the high diversity is maintained. The existence of specific competition mechanisms provides a possible explanation of this alternative community behavior. Preliminary experiments demonstrate the existence of sponge toxins (allelochemicals) capable of halting feeding or causing mortality of ectoprocts. Circumstantial evidence suggests allelochemical interactions exist among all other major colonial animal groups on the reef. Allelochemical effects appear quite specific as no sponge causes mortality

or cessation of feeding in all ectoproct species subjected to the sponge.

Existence of specific competition mechanisms suggests an alternative but complementary model for maintenance of diversity in space-limited systems in the absence of high levels of disturbance. The model requires that interference competitive ability of space-occupying organisms does not follow a simple linear-ranked hierarchy. Such systems may instead be structured by competitive networks (Species A > Species B > Species C but Species C > Species A) as opposed to competitive hierarchies.

The more species and the more numerous and complex the competitive networks of any such system, then the slower will space tend to be occupied by a single competitive dominant, and the less the amount of external disturbance necessary to maintain a given level of diversity within the system. Research this summer has demonstrated that competitive networks are present in both cryptic and exposed reef environments. The major question that now emerges is why are some systems characterized by linear hierarchies and others by networks.

THE IMPORTANCE OF STRUCTURAL HETEROGENEITY
IN A MARINE INFANAL SYSTEM

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The distribution and abundance of an infaunal assemblage located intertidally (-0.03 m tidal height) in Tom's cove, Assateague Island, Virginia was investigated. Samples were taken monthly from March 1974 to October 1975. The assemblage is dominated numerically and taxonomically by polychaete annelids. The numerically dominant species are members of the families Spionidae (*Spio* spp. and *Streblospio benedicti*), Chaetopteridae (*Spiochaetopterus oculatus*), and Cirratulidae (*Tharyx acutus*). *Diopatra cuprea*, an onuphid polychaete, is the most conspicuous organism due to its size and large epifaunal tube cap. To determine the effect of *Diopatra* on the remainder of the infauna, samples were taken from areas with and without *Diopatra*. The tube cap was sampled separately. The abundance of infauna increases significantly with increases in the abundance of *Diopatra*. Samples taken in a concentric ring design showed that this increase was restricted to the inner 0.01 m² x 16 cm sample. To separate the effect of the worm, *Diopatra*, from that of its tube and tube cap, artificial high density (6/0.01 m²) *Diopatra* areas were created using a combination of stakes and plastic straws. The straws were bent and placed on stakes in the sediment in 0.01 m² areas without *Diopatra*. After 5 months the infaunal abundances in these areas were not significantly different from abundances in natural areas with identical densities of real *Diopatra*. Thus, the effect is due to the presence of the tube, not the worm.

Predator exclosures were used to test the hypothesis that the significant increase in infaunal abundance with the presence of *Diopatra* tubes was due to a reduction in

¹This research was supported in part by NSF Grant no. GA-42611.

predation pressure. No significant differences were observed among infaunal densities in the sideless exclosures, topless exclosures, and control areas. Infaunal abundances increased significantly, however, within the completely enclosed areas relative to densities in the control areas; the differences in density due to presence or absence of *Diopatra* disappeared. This was not true of exclosures that failed to exclude the main predator, *Callinectes sapidus*. The significant increase in infaunal abundances with high densities (6/0.01 m²) of *Diopatra cuprea*, then, is due to the presence of the tube, not the worm, and to reductions in predation pressure associated with the presence of the tube.

STRUCTURE OF TWO SOFT-BOTTOM, ULTRA-ABYSSAL COMMUNITIES

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In the last five years, the deep-sea benthic program at Scripps Institution of Oceanography has had the opportunity of sampling ultra-abyssal sediment ponds in the axes of two trenches: the Aleutian Trench at 7300 meters, and the Philippine Trench at 9600 m. Unlike most programs in the past, we have concentrated on small-scale sampling devices, which emphasize the interactions of individuals rather than populations. While the samples are few, they reveal conditions that are sufficiently clear-cut to warrant discussion.

A 0.25 m² box core from the Aleutian Trench displayed a standing crop as high (1272 ind./m²) as is found at bathyal depths along continental margins. The species diversity of this sample is very low, much lower than is typical for other deep-sea communities. These features can be explained in terms of food supply and environmental stability, which are factors that have been strongly implicated in the control of deep-sea communities in general. The high standing crop is a result of the high regional productivity of overlying waters. The low diversity is most probably an outcome of the highly unstable sedimentary regime, where frequent seismic activity interacts with a high sedimentation rate to produce sporadic, catastrophic deposition at a rate which is high compared to the recovery time of the community.

The Philippine Trench samples also display low diversity, and sedimentological cores show repeated graded bedding as documentation of the unstable depositional conditions. Here standing crop is much lower, reflecting a lower nutrient input which results either from lower surface productivity or the great depth of water.

The taxonomic composition of the Aleutian Trench sample shows unusual relative abundance of aplacophorans, enteropneusts and echiurids, compared to other deep-sea communities. Echiurids are also unusually abundant in the Philippine Trench. Too little is known of the autecology

of these taxa to explain these relationships.

Baited camera and trap samples from the Philippine Trench show another unusual aspect of taxonomic composition at ultra-abyssal depths. Tremendous numbers of amphipods were attracted to the dead fish used as bait. This stands in contrast to abyssal and bathyal depths, where fish and decapods comprise the major portion of the biomass which is attracted. Once again, there is no ready explanation for this difference. It is always possible that the great hydrostatic pressure has an adverse effect on fish and decapods. However, there is also the possibility that the amphipods have gained a strong selective advantage from a shift in the nature of the food supply.

A COMPARISON OF EAST AND WEST COAST POPULATIONS OF A
NUDIBRANCH-ANEMONE ASSOCIATION WITH EMPHASIS ON FORAGING
STRATEGIES AND THE INFLUENCE OF ENVIRONMENTAL STABILITY

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The anemone-eating nudibranch *Aeolidia papillosa* is found associated with subtidal populations of the acontiate anemone *Metridium senile* along the Atlantic and Pacific coasts of the United States. There are striking differences in the dynamics of east and west coast populations of *Aeolidia* which in turn influence the population structure of *Metridium*. East coast populations of *A. papillosa* undergo large seasonal fluctuations with high numbers of adult individuals present through the winter and most reproduction occurring in the spring. The decline of *Aeolidia* populations is correlated with increased foraging by crabs and bottom-feeding fishes. *Metridium senile* has an effective defensive response to *Aeolidia* predation in the extrusion of nematocyst-bearing acontia; the defensive response is directly correlated to the damage caused by the attacking nudibranch. Young *Aeolidia* initially attack large anemones and shift to smaller anemones when the response from large anemones becomes too intense. The result of the foraging strategy of *Aeolidia* is that only large anemones which are relatively immune to attack survive outside of aggregations and *Metridium* populations typically consist of large solitary individuals and aggregates of large and small individuals.

West coast populations of *Aeolidia* are nonseasonal with reproduction occurring throughout the year. Populations of *Aeolidia* are dominated by young nonreproductive individuals as is typical of a predation-regulated population. West coast *Metridium* populations are less tightly aggregated and the mean size of the anemones is smaller, suggesting that *Aeolidia* populations are suppressed by predation below that which would seriously affect *Metridium* populations.

Laboratory studies have shown that *A. papillosa* prefers

to eat most temperate anemone species over *Metridium senile*. However, large populations of *Aeolidia* are found only in association with *Metridium*. It is suggested that preferred anemone species utilize one or more escape mechanisms such as intertidal distribution, solitary habit and/or active escape responses which have made it evolutionarily impossible for *Aeolidia* to develop a larval preference for these preferred anemones over the common, aggregated, subtidal *Metridium senile*.

East and west coast populations of *Aeolidia* are predator controlled. Populations in the highly seasonal, low diversity east coast communities show regular but extreme oscillations. In contrast, west coast populations are much more stable and the community structure is more complex and shows less seasonal variation. The results of this comparative study are cited as evidence for the validity of the Stability-Time Hypothesis. It is also suggested that there is an inverse correlation between community resilience and community complexity.

ECOLOGICAL IMPLICATIONS OF PATTERNS OF ROCKY
INTERTIDAL COMMUNITY STRUCTURE AND BEHAVIOR
ALONG AN ENVIRONMENTAL GRADIENT

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Much current ecological research is aimed at understanding how community structure arises and persists. Two key problem areas in this quest are (1) species diversity gradients, and (2) community stability. I discuss a graphic model which suggests that species diversity patterns along environmental gradients are a function of both competitive interactions (among species in the top trophic level) and predation (acting on species in the lower trophic levels). The relative overall importance of these interactions on community structure is inversely correlated and depends on environmental rigor. In rigorous (relatively variable, unpredictable, stressful) environments, trophic structure is simple (few trophic levels) and competition has the greatest effect on community structure. In more benign (less variable, more predictable, non-stressful) environments, trophic structure is more complex because the physiologically more delicate predators are not as inhibited by the physical environment. In such communities predation has the greatest overall effect on community structure and competition is important in organizing guilds of top predators. In the most structurally and trophically complex communities, competition may also have an important regulatory effect at the lowest trophic levels because species at these levels appear to escape control by their (middle level) predators, who in turn are controlled by the top predators. Experiments supporting the predictions of this model, mostly from rocky intertidal systems, are briefly discussed.

Communities occurring in highly stable physical environments are thought to have high persistence stability and low adjustment stability, while communities in unstable environments theoretically have low persistence and high resilience. Data from the New England rocky intertidal are presented which seem to support these hypotheses. I suggest that

these patterns of community behavior result from (1) differences in life history characteristics of structurally dominant species, and (2) differences in the intensity of biological interactions, especially those between consumers and their prey. Thus, communities in unstable environments have relatively high resilience but low persistence because the structurally dominant species are relatively opportunistic (early maturing, short-lived, fast growing, high recruitment rates) and are unaffected by predation. Communities in stable environments have low resilience but high persistence because the structurally dominant species are relatively longevous (late maturing, long-lived, slow growing, low recruitment rates) and predation intensity is intense and chronic, greatly reducing the frequency of escapes by the structural dominants.